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Puellina (Bryozoa; Cheilostomata; Cribrilinidae) from British and adjacent waters

J. D. D. Bishop & B. C. Household

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Synopsis

Cribrilaria Canu & Bassler, 1929 is treated as a subgenus of *Puellina* Jullien, 1886, and *Glabrilaria* n.subgen. is established within *Puellina* to accommodate *P. pedunculata* Gautier, 1956 and related species. The following nine species of *Puellina* are recognised from British and adjacent waters: *P. arrecta* n.sp., *P. bifida* (d'Hondt, 1970), *P. corbula* n.sp., *P. directa* n.sp., *P. gattyae* (Landsborough, 1852), *P. innominata* (Couch, 1844), *P. modica* n.sp., *P. praecox* n.sp., and *P. venusta* Canu & Bassler, 1925. A table of key characters for the identification of these species is given. The distribution of *Puellina* around the British Isles shows a marked southerly and westerly bias. There seems to be no evidence for the occurrence of *P. setosa* (Waters, 1899) further north than the southern part of the Bay of Biscay.

A neotype is designated for *P. gattyae*. Lectotypes are selected for *Lepralia steindachneri* Heller, 1867 and *L. cribrosa* Heller, 1867, both of which are junior synonyms of *P. gattyae*, and for *P. setosa, P. bifida, P. pedunculata* and *P. flabellifera* (Kirkpatrick, 1888).

P. praecox n.sp. also occurs in the Plio-Pleistocene Red Crag of eastern England. *P. venusta* is found as a fossil in the Badenian (Middle Miocene) of the Vienna Basin. *P. bifida* is extremely similar to *P. kollmanni* (David & Pouyet, 1974) from the Badenian of the Vienna Basin. *P. rarecostata* (Reuss, 1848) from the same rocks is intermediate in appearance between the two Recent species *P. setosa* and *P. modica*.

Three categories of ovicell development within the genus are noted, and their significance discussed.

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Introduction

Perhaps because of difficulties of observation caused by their small zooid size, there has been a tendency in the past to assign most Recent *Puellina* or *Cribrilaria* specimens to a limited number of nominal species within which extensive morphological variation has been accommodated. The wide limits of variation assigned to *Cribrilina radiata* by Hincks (1880) is a notable example of this approach. The subsequent task of refining species concepts within the group has been given impetus by the increased morphological detail available through the use of the Scanning Electron Microscope (SEM). This work was initiated by Harmelin (1970) in a revision of Mediterranean species and has been continued by the same author (1978; 1984) for NE. Atlantic and Mediterranean faunas.

The present paper is an account of Recent species from British and adjacent waters, in which mention is also made of relevant fossil material from the European Neogene. Following Gordon (1984), *Cribrilaria* is treated as a subgenus of *Puellina*. A new subgenus within *Puellina* is established for certain species formerly placed in *Cribrilaria*.

Material and methods

Material studied during the present work is located in the following institutions:

BMNH: British Museum (Natural History), London, U.K.; Recent specimens, Zoology Department; fossil specimens, Palaeontology Department.

IP: Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France; Canu Collection.

IZUI: Institut für Zoologie der Universität Innsbruck, Innsbruck, Austria; Heller Collection.

Table 1 Details of Channel Stations

Station	Latitude	Longitude	Depth	Deposit
183	50°39·3′N	01°22·6′E	48 m	Clean coarse sand
230	49°36·3′N	03°26·7′W	75 m	Coarse shell sand
240	49°30·4′N	01°59·0′W	29 m	Coarse shell sand
247	49°10·8′N	02°52·1′W	64 m	Clean fine shell gravel, some stones
248	49°08·1′N	03°02·3′W	73 m	Clean fine shell gravel, some stones
249	49°05·1′N	03°13·5′W	77 m	Clean fine shell gravel, some stones
250	49°02·5′N	03°25·0′W	80 m	Stones, some clean fine shell gravel
251	49°00·0′N	03°36·5′W	77 m	Coarse shell sand, some stones
252	48°57·0′N	03°48·7′W	82 m	Clean shell gravel, some stones
253	48°52·2′N	03°54·0′W	79 m	Clean coarse sand, some gravel
256	48°50·7′N	04°13·1′W	91 m	Clean coarse shell sand, some stones
257	48°48·7′N	04°22·5′W	96 m	Clean coarse shell sand, some stones
258	48°46·2′N	04°30·7′W	99 m	Clean coarse shell sand, some stones
260	48°51·5′N	04°42·0′W	106 m	Coarse silty sand, some gravel and stones
261	49°00·0′N	04°44·5′W	101 m	Clean coarse shell sand, some gravel and stones
263	49°15·2′N	04°50·0′W	102 m	Coarse silty shell sand, some shells
275	49°38·2′N	01°00·0′W	38 m	Clean coarse sand, some gravel and stones
314	49°12·4′N	03°14·8′W	73 m	Clean shell gravel, some stones
315	48°57·5′N	04°00·7′W	88 m	Clean fine shell gravel, some stones
316	49°07·2′N	04°02·5′W	86 m	Stones, some clean fine shell gravel
317	49°18·0′N	04°04·2′W	86 m	Shell gravel, some stones
318	49°27·6′N	04°07·0′W	86 m	Clean coarse shell sand, some stones

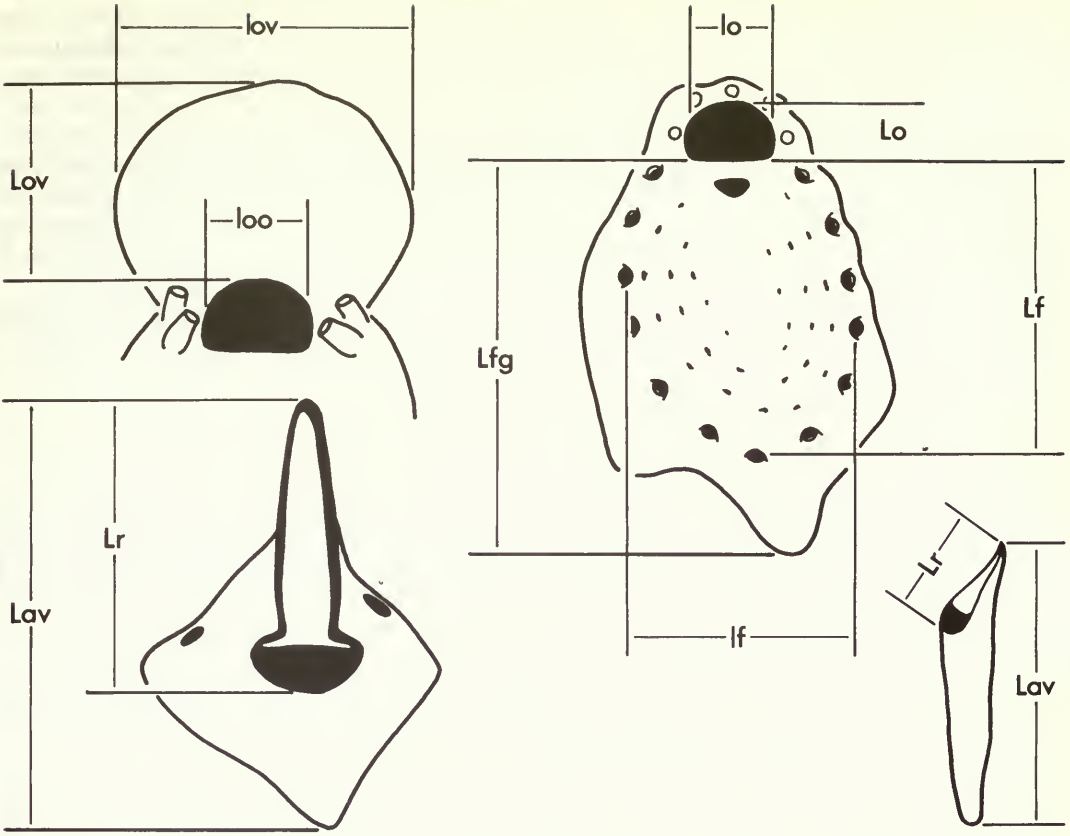


Fig. 1 Measurements on autozooids, interzooidal avicularia (bottom left) and erect avicularia (bottom right). Abbreviations: Lav = length of rostrum and frontal non-calcified area plus proximal gymnocyst of avicularium; Lf = length of frontal shield of autozooid; lf = width of frontal shield of autozooid; Lfg = length of frontal shield plus gymnocyst of autozooid; Lo = length of orifice of non-ovicellate autozooid; lo = width of orifice of non-ovicellate autozooid; loo = width of orifice of ovicellate autozooid; Lov = length of ovicell; lov = width of ovicell; Lr = length of rostrum plus frontal non-calcified area of avicularium.

LBIMM: Laboratoire de Biologie des Invertébrés Marins et de Malacologie, Muséum National d'Histoire Naturelle, Paris, France.

MM: Manchester Museum, Manchester, U.K.; microslide preparations from the Waters Collection.

NMV: Naturhistorisches Museum, Vienna, Austria.

Many of the records presented here are from encrusted shells collected during 1960 to 1962 for a study of the Recent benthos of the English Channel by Holme (1966), subsequently used for an account of bryozoan assemblages by Grant & Hayward (1986), and now deposited in the collections of the BMNH. Station details taken from Holme (1966) are given in Table 1. In the list of material examined for each species, these stations are referred to simply as 'Channel Stn . . .'; they are mostly on the French side of the Channel, with a few in mid-Channel. Locality details of other BMNH material are given as they appear on specimen labels or in the specimen catalogue; any additional information is given in square brackets.

SEM observations were made on uncoated material using an International Scientific Instruments model 60A with charge-free anticontamination system (CFAS). Images were generated at a

working voltage of 15 or 25 KV from back-scattered electrons using a Robinson detector. The magnifications of the resulting micrographs were calculated by light microscope calibration of each specimen, since the readings given by the SEM itself were inaccurate. Stereo pairs were taken at an angular separation of 10°.

Morphological measurements were taken from scanning electron micrographs. The measurements, and the abbreviations employed for them, are explained in Figure 1. Orifice width was measured to the proximo-lateral corners of the orifice. The papilla pores were taken to mark the edge of the frontal shield. Ovicell length was measured to the distal margin of the ovicell opening. The apertural bar was not included in counts of the number of costae. Values of the coefficient of variation (C.V.) were corrected as described by Simpson, Roe & Lewontin (1960:101, 102).

The term pluriserial is used in the descriptions below to indicate encrusting colonies forming lobes of fewer than about 10 autozooids abreast (Figs 29, 74). Multiserial colonies consist of broader lobes or extensive sheet-like growths.

Ovicell development

In *Puellina*, and in many other cribrimorphs, the process of colony growth is apparently discontinuous, with pauses between the budding of successive zooid generations at the edge of the colony (Lidgard, 1985). Based on the timing of production of the ovicell in relation to the budding of the maternal autozooid and of the zooid distal to it, the following three categories of ovicell may be recognised in the species discussed here:

A—The ovicell is produced during the budding of an autozooid distal to the maternal autozooid, and is a proximal component of the distal autozooid. Thus the completed ovicell never lies at the extreme edge of the colony. The frontal walls of the ovicell and of the distal autozooid are continuous. See Figures 40, 46, 50, 62 and 79.

B—The ovicell is produced during the budding of a kenozooid (which has an area of costate frontal shield) distal to the maternal autozooid, and is a proximal component of the kenozooid. If the area of costate frontal shield is relatively small, the newly completed ovicell may lie very close to the extreme edge of the colony. The frontal walls of the ovicell and of the kenozooid are continuous. See Figures 70, 94, 95 and 96.

C—The ovicell appears to be a distal component of the maternal autozooid, and is not associated with an area of kenozooidal costate frontal shield. Thus the newly completed ovicell lies at the extreme edge of the colony. Zooids distal to the maternal autozooid and ovicell are budded subsequently, and their frontal walls are separate from that of the ovicell. See Figures 2, 19, 23, 33 and 83.

Ovicells of category C of certain species have a number of uncalcified subcircular spots on the frontal surface (Figs 2, 12), similar in appearance when viewed by SEM to the pelmatidia of the costate frontal shield. These occur in a more or less regular arrangement, generally approximating to an outer ring of spots sometimes enclosing a number of others. This condition is referred to as punctate in the relevant descriptions below. In ovicells of category C of other species, and of categories A and B, small uncalcified patches sometimes occur on the frontal surface (Figs 50, 73), particularly on the crests of ridges and the tops of tubercles. However the size, shape and occurrence of these patches are inconstant and their spatial arrangement is relatively haphazard, and in such cases the ovicell is described below as non-punctate.

Systematic account

Genus *PUELLINA* Jullien, 1886

Type species: *P. gattyae* (Landsborough, 1852), by original designation.

Jullien (1886), in addition to establishing *Puellina*, selected *Eschara radiata* Moll, 1803 as the type

species of *Cribrilina* Gray, 1848. Since *Lepralia punctata* Hassall, 1841 is the type species of *Cribrilina* by monotypy, Jullien's selection was invalid, but it did serve to indicate clearly that he excluded *E. radiata* from the genus *Puellina*. However, *E. radiata* is the type species of *Cribrilaria* Canu & Bassler, 1929, which is treated in the present paper as a subgenus of *Puellina*. The definition of the genus *Puellina* adopted here is therefore broader than Jullien's (1886), but coincides with that of Levinsen (1909), who referred *E. radiata* to the genus, and of Gordon (1984), who included *Cribrilaria* in *Puellina* as a subgenus. Jullien's original concept of the genus was in fact equivalent to that of the subgenus *Puellina* employed here.

REVISED DIAGNOSIS. Autozooid with pericystal frontal shield of fused but discernible spines (=costae) in more or less pinnate or radiating pattern; each costa generally with 1 or more small pelmatidia (=lumen pores); fusion of successive costae interrupted by 1 or more lacunae (=intercostal pores) which are short (i.e. do not take a slit-like form elongate parallel to the costae); non-calcified papilla (presumed to be evagination of frontal membrane) protruding from single papilla pore (bordered on one side by gymnocyst) between bases of successive costae around margin of frontal shield. Calcified (secondary) orifice D-shaped, with straight proximal edge, abutting similarly-shaped operculum around its entire margin; orifice without condyles, operculum hinged at extreme proximal edge. Apertural bar (presumed to be modified distalmost pair of costae) just proximal to orifice usually with 1 or more sub-oral (=sub-orificial) lacunae on midline between left and right components of bar. Oral (=orificial) spines erect, unfused, jointed at or near base, present around lateral and distal margins of orifice in non-ovicellate autozooids, restricted to lateral margins of orifice in ovicellate zooids. Autozooids with several pore chambers around distolateral and distal margins. Ovicell sub-globular, hyperstomial, cleithral. Avicularium (if present) with discrete gymnocystal cystid. Ancestrula tatiform, without pronounced cryptocyst, frequently regenerated as zooid with cribrimorph frontal shield.

The possession of non-calcified papillae protruding through papilla pores around the periphery of the frontal shield is regarded here as a synapomorphy of the genus *Puellina*.

Subgenus *PUELLINA* Jullien, 1886

Puellina Jullien, 1886; 607.
Puellina: Prenant & Bobin, 1966; 597. Hayward & Ryland, 1979; 66. Harmelin, 1984; 81.

Type species: *P. gattyae* (Landsborough, 1852), by original designation. Other NE. Atlantic species included: *P. setosa* (Waters, 1899), *P. modica* n. sp.

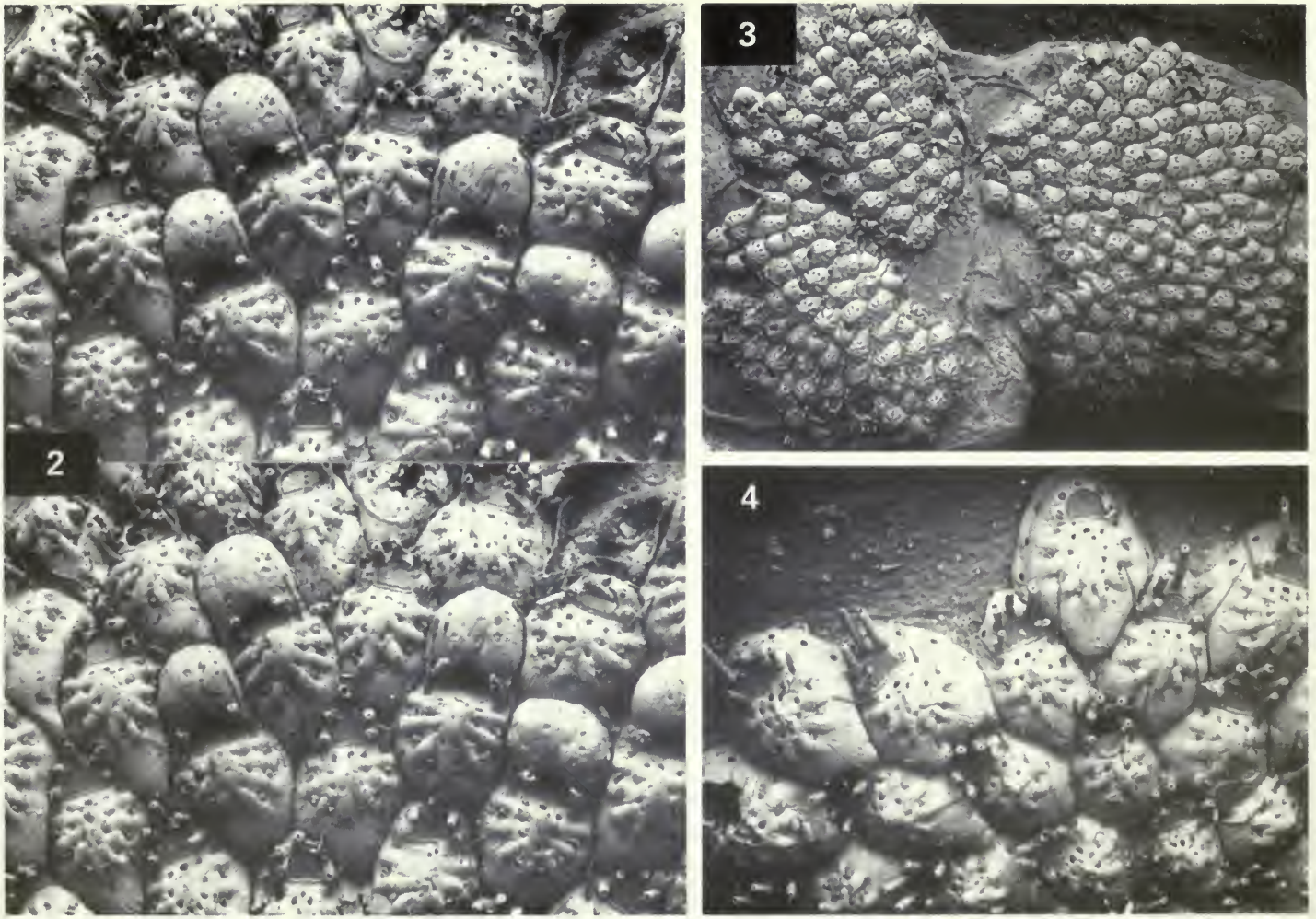
Proximal gymocyst of autozooid relatively broad; pericyst relatively small (approximately circular in outline). Oral spines without apophyses, each with brown chitinous articulation at base; 2 spines in ovicellate zooids (5 in non-ovicellate zooids). Setiform papillae from most distal pair of papilla pores. External uncalcified windows of pore chambers relatively small. Ovicell of category C (p. 4), punctate. No avicularia. Median proximal spine of ancestrula with simple (not bifid) tip; ancestrula regenerated as miniature autozooid (or kenozooid).

Subgenus *CRIBRILARIA* Canu & Bassler, 1929

Cribrilaria Canu & Bassler, 1929; 33. (*Cribrilaria* Canu & Bassler, 1928; 27 is regarded as a *nomen nudum*.)
Cribrilaria: Hayward & Ryland, 1979; 62. Gordon, 1984; 63.

Type species: *P. radiata* (Moll, 1803), by original designation. NE. Atlantic species included: *P. venusta* Canu & Bassler, 1925, *P. innominata* (Couch, 1844), *P. bifida* (d'Hondt, 1970), *P. hexaspinosa* (Harmelin, 1978), *P. octospinosa* (Harmelin, 1978), *P. arrecta* n.sp.

Proximal gymnocyst of autozooid relatively narrow; pericyst relatively large. Oral spines with or without apophyses, bases not brown; 4 in ovicellate zooids. Setiform papillae from most distal pair of papilla pores. External uncalcified windows of pore chambers relatively large. Ovicell of category A (p. 4) (sometimes B in *P. bifida*), non-punctate. Avicularia interzooidal. Median proximal spine of ancestrula generally with bifid tip; ancestrula regenerated as kenozooid.



Figs 2–4 *Puellina gattyae* (Landsborough): (2) stereo pair of neotype (BMNH 1854.11.15.125), Sidmouth, ×81; (3) whole colony, neotype, ×19; (4) edge of colony, BMNH 1897.5.1.623, South Devon, ×80.

Subgenus *GLABRILARIA* n.subgen.

Type species: *P. pedunculata* Gautier, 1956. Other species included: *P. africana* (Hayward & Cook, 1983), *P. corbula* n.sp., *Cribrilaria pedunculata* in the sense of Harmelin (1968) (not Gautier, 1956), *P. cristata* (Harmelin, 1978).

Proximal gymnocyst of autozooid relatively narrow; pericyst relatively large. Oral spines without apophyses, bases not brown; 4 in ovicellate zooids. Ordinary (short) papillae from most distal pair of papilla pores. External uncalcified windows of pore chambers of moderate size. Ovicell of category B or C (p. 4), non-punctate. Avicularia small, erect or semi-erect, generally budded from single pore chamber. Median proximal spine of ancestrula with simple (not bifid) tip; ancestrula regenerated as kenozooid.

ETYMOLOGY. From a modification of *Cribrilaria*, from which the new subgenus is distinguished, combined with the Latin *glaber*, 'without hair' or 'smooth skinned', a reference to the absence of setiform papillae in this group.

Puellina (Puellina) gattyae (Landsborough, 1852)

(Figs 2–10 and Table 2)

Lepralia gattyae Landsborough, 1852; 326, 327, pl. 18 fig. 71.
Lepralia gattyae: Busk, 1854; 73, 74, pl. 83 fig. 6.
Lepralia steindachneri Heller, 1867; 109, 110, pl. 2 fig. 5.
Lepralia cribrosa Heller, 1867; 109, pl. 2 fig. 6.
Lepralia gattyae: Waters, 1879; 36, pl. 9 fig. 6.
Cribrilina gattyae: Hincks, 1880; 198, 199, pl. 25 fig. 10.
not *Cribrilina gattyae*: Norman, 1903; 98 (as '*Gattyae*') 'form encrusting a shell', pl. 9 fig. 5.
not *Puellina gattyae* var. *balearica* Barroso, 1919; 340, 341, figs 1–5 (= *Collarina* sp.).
Puellina gattyae: Prenant & Bobin, 1966; 598–600, fig. 208I.
Puellina gattyae: Hayward & Ryland, 1979; 66, 67, fig. 18A–D.
Puellina gattyae: Harmelin, 1984; 81–82, 85–87, figs 2–4, 7.

MATERIAL EXAMINED BY SEM.

Neotype (designated here): BMNH 1854.11.15.125 (Sidmouth, [South] Devon).

BMNH: 1897.5.1.623 (South Devon, three colonies); 1899.7.1.1317A (Sidmouth); 1911.10.1.735A (Belfast, on shell).

IZUI: 135/9855 (Adriatic Sea, lectotype of *Lepralia steindachneri* Heller, 1867, selected here); 125/17021 (Adriatic Sea, lectotype of *Lepralia cribrosa* Heller, 1867, selected here).

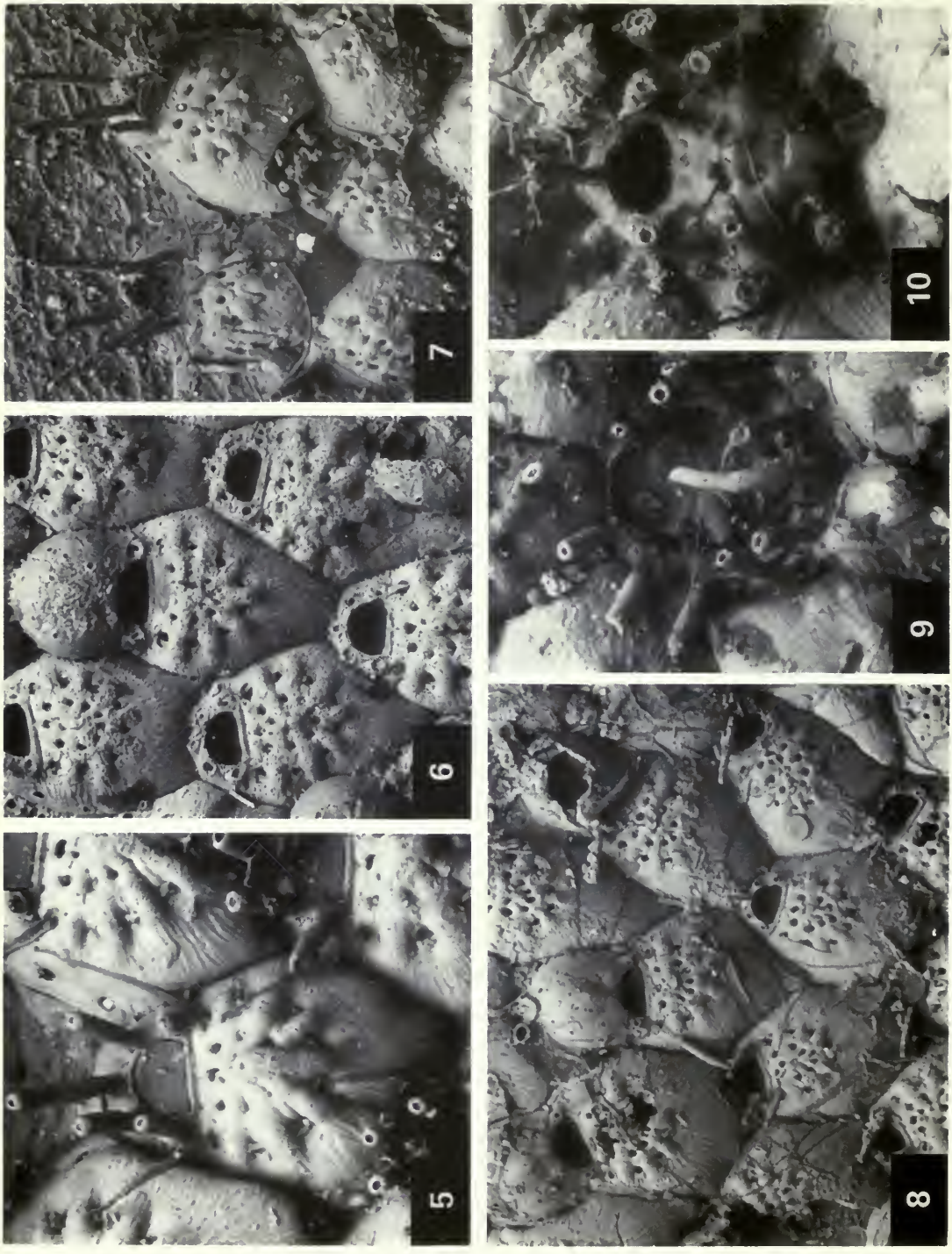
OTHER MATERIAL.

BMNH: 1879.4.25.17 (Naples); 1899.5.1.717 (Birterbuy [= Bertraghboy] Bay [Galway], labelled *Cribrilina punctata* var., colony on shell fragment 1); 1899.7.1.1317 and 1899.7.1.1318 (Sidmouth); 1899.7.1.1319 (Weymouth); 1911.10.1.734 (Naples); 1911.10.1.736 (British); 1975.1.12.444, 1975.1.12.518–522, 1975.7.1.5 and 1975.7.1.10 (Chios).

MM: 987 and 988 (Naples); 992 and 1171 (Menton).

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material multiserial, with a few hundred autozooids. Autozooid of variable shape in frontal view, generally sub-oval (longer than broad). Lateral gymnocyst of autozooid narrow or of moderate width; proximal gymnocyst broad, with proximal extension(s) between neighbouring zooids; gymnocyst with fine radiating striations.

Frontal shield (= pericyst) generally almost circular in outline, moderately to heavily calcified, slightly to strongly convex, with 5–9 costae (usually 7 or 8) fused extensively in centre of shield; central region of costal fusion may form blunt median umbo (frequently well developed in ovicellate zooids; Fig. 2). Each costa generally without clearly differentiated basal and subsequent portions, without distinct ornamentation; minute pelmatidium frequently seen near base, and larger pelmatidium occasionally near centre of shield. Intercostal pores subcircular, of variable size, without denticles, usually only 1 pore between successive costae. Lipped papilla pore between bases of successive costae, larger than adjacent intercostal pore.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Orifice of non-ovicellate autozooid D-shaped, clearly broader than long, proximal edge straight. Orifice of ovicellate zooid not appearing truncate in frontal view; width 1·1–1·2 times that of orifice of non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid (6 in one disrupted autozooid of neotype), 2 in ovicellate zooid; with brown chitinous joint at base but without subsequent segmentation, without apophyses. Apertural bar sloping upwards to variable extent from proximal margin of orifice to first pair of costae; without tubercles; median suture and minute pelmatidium either side of midline occasionally discernible. Single median sub-oral lacuna, of variable shape and size although generally slightly larger than an intercostal pore, without denticles, flanked on either side by single intercostal pore (occasionally 2) slightly proximal to it.

Each autozooid with 6–8 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony: Fig. 4) relatively small (about size of sub-oral lacuna).

Ovicell of category C (p. 4), length 1·0–1·2 times that of frontal shield of autozooid; frontal surface punctate, without ridges or discernible median suture.

Avicularium not present in available material.

Ancestrula (Fig. 9) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Erect spines jointed at base; details of subsequent jointing (if any) not seen. Median proximal spine blunt-tipped and of relatively uniform thickness throughout length. Spines without inwardly directed (or other) apophyses. Ancestrula sometimes regenerated as small autozooid with 3 or 4 oral spines (Fig. 10).

Table 2 *Puellina gattyae* (Landsborough): measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	47–51	48·7	3·17	9	Lf	99–150	130	8·87	24
b		45–53	48·1	6·32	8		124–155	140	10·0	10
c		42–49	45·5	12·3	2		88–97	94·0	5·99	3
d		43–47	44·4	4·43	7		100–148	124	11·5	15
a	lo	59–66	62·7	4·29	6	Lfg	193–301	235	13·2	24
b		65–70	67·6	3·55	8		237–390	279	19·3	10
c		56–60	58·0	5·49	2		193–222	211	8·18	3
d		57–75	64·4	15·8	5		218–346	273	14·9	14
a	loo	70–87	77·8	7·63	4	lf	115–169	140	10·5	24
b		85–88	86·5	2·76	2		108–147	132	8·80	10
c		—	—	—	0		84–111	94·3	16·8	3
d		72–87	80·3	7·21	7		93–157	125	18·3	15
a	Lov	123–155	138	8·14	10	lov	158–190	176	4·96	10
b		144–155	147	2·64	8		166–187	176	4·48	9
c		—	—	—	0		—	—	—	0
d		134–171	148	9·68	6		154–179	165	5·76	7

a = neotype (BMNH 1854.11.15.125); b = BMNH 1911.10.1.735A; c = IZUI 9855 (lectotype of *Lepralia steindachneri* Heller); d = IZUI 17021 (lectotype of *Lepralia cribrosa* Heller).

Figs 5–10 *Puellina gattyae* (Landsborough): (5) non-ovicellate autozooid, BMNH 1897.5.1.623, South Devon, × 163; (6) ovicellate and non-ovicellate autozooids, BMNH 1911.10.1.735A, Belfast (on shell), × 113; (7) non-ovicellate autozooids, IZUI 135/9855, Adriatic (lectotype of *Lepralia steindachneri*), × 123; (8) ovicellate and non-ovicellate autozooids, IZUI 125/17021, Adriatic (lectotype of *Lepralia cribrosa*), × 101; (9) ancestrula, BMNH 1897.5.1.623, South Devon, × 240; (10) ancestrula regenerated as autozooid, BMNH 1899.7.1.1317A, Sidmouth, × 290.

REMARKS. Type material of *Puellina gattyae* does not seem to have been formally recognised by previous authors. Despite this, there has apparently been little uncertainty concerning the identity of *P. gattyae* occurring on algae, although the synonyms *steindachneri* and *cribrosa* were created by Heller (1867), and Barroso (1919) erroneously assigned a new variety to the taxon. However there has been confusion, outlined below, regarding the occurrence of the species on hard substrata. *P. gattyae* also has at least two very close relatives, *P. setosa* (which has been the subject of considerable taxonomic uncertainty itself) and *P. modica* n.sp. Therefore an evaluation of possible type material is now considered worthwhile.

Landsborough (1852:326) introduced the name *Lepralia gattyae*, but attributed the name to Busk. Landsborough's description of the species was preceded by quotation marks and was stated (1852:326) to be 'from the pen of Mrs. Gatty', who, furthermore, was credited with the discovery of the species. It had been found (1852:327) on algae 'during two successive winters, at Sidmouth (1851 and 1852), and is to be met with also in Jersey'. Landsborough's figure (but not his text) was cited in Busk's (1854) account of *L. gattyae*; again the discovery of the species was credited to Mrs Gatty and material was reported from the same two localities, Sidmouth (Mrs Gatty) and Jersey (J. Alder).

Hence it would appear that the original concept of the species employed by both Landsborough and Busk was due to Mrs Gatty, and that the name *gattyae* was probably suggested to Landsborough by Busk. Despite the fact that Landsborough's use of the name appeared first, Busk has been cited, incorrectly, as the author of *Lepralia gattyae* by several subsequent workers, including Hincks (1880), Jullien (1886), Waters (1899), Levinsen (1909), Barroso (1919) and Eggleston (1969). No collection of material associated with Landsborough's work is known. The Busk collection at the BMNH does not contain any material of the species from Jersey and only one microslide preparation, BMNH 1854.11.15.125, a single colony on alga from Sidmouth provided by Mrs Gatty, is undoubtedly contemporary with Busk's catalogue (1854). The label reads: 'Sidmouth G L. ['coronata' crossed out] Gattyae Pl. 83'. The letter 'G' on the label identifies Mrs Gatty as the source of the specimen, as may be confirmed by checking other microslides with this mark against the entries in Busk's catalogue; *Flustra coronata* Audouin had been likened by Busk (1854) to *L. gattyae*; plate 83 refers to the illustration of *L. gattyae* in Busk (1854). However, BMNH 1854.11.15.125 is not recognisable as the colony illustrated by either Landsborough or Busk. It is noted as 'type' in the MS species catalogue of the BMNH, but this supposed type status is presumed to stem from the specimen's connection with Busk's (1854) account rather than Landsborough's (1852). Although it is probable that this colony was part of the material on which Mrs Gatty based her description of the species published by Landsborough, it is not possible to prove this conclusively and it would not be valid to select it as lectotype. However, BMNH 1854.11.15.125 is clearly the best available indicator of the true nature of Landsborough's species, and in recognition of its significance it is selected here as neotype. The colony has lost much of its earlier growth, leaving two almost disjunct lobes totalling *c.* 200 autozooids.

Examination of IZUI specimen 135/9855 (Fig. 7) confirmed the conspecificity of *Lepralia steindachneri* Heller, 1867 and *P. gattyae*; this was first suggested by Waters (1879) and has been generally accepted by later authors. The arrangement of zooids in IZUI 135/9855 is reminiscent of Heller's plate 2 figure 5, but is not precisely the same; it is not known if this is the illustrated specimen. However, no other material attributable to Heller's account of this species is known (W. Schedl, Institut für Zoologie der Universität Innsbruck, pers. comm. to JDDB, 1986) and specimen 135/9855 is hereby selected as lectotype of *L. steindachneri*, confirming the established synonymy.

The identity of *L. cribrosa* Heller, 1867 has been uncertain in the past, but the name has been commonly cited as a junior synonym of *Collarina balzaci* (Audouin). However, Heller's figure (1867: pl. 2 fig. 6) shows setiform papillae, which are not present in *C. balzaci* auct. The type material received on loan (IZUI 125/17021; Fig. 8) is in fact referable to *P. gattyae*. Once again, it is not known if this is the specimen illustrated by Heller, but no other material referable to Heller's account is available (W. Schedl, Institut für Zoologie der Universität Innsbruck, pers. comm. to JDDB, 1986). IZUI 125/17021 is therefore selected as lectotype of *L. cribrosa*, the name of which passes into the synonymy of *P. gattyae*. Heller's Adriatic material (of both nominal species) and

the BMNH specimens from the Aegean (Chios) listed above have a relatively smaller, flatter, and more lightly calcified frontal shield than is generally seen in material from further west in the Mediterranean basin and from the NE. Atlantic. In the Chios specimens, the median umbo may be relatively narrow and pointed.

Whilst there has been little confusion concerning the identity of *P. gattyae* material growing on algae, the name has been applied to several taxa encrusting shells etc., apparently in the belief that the appearance of the species is transformed on hard substrata. In fact *P. gattyae* on shell (BMNH 1899.5.1.717 and 1911.10.1.735A: Fig. 6) looks much the same as on algae and has similar dimensions (Table 2). Norman (1903) contrasted a form he tentatively attributed to *P. gattyae* found on a shell from Guernsey with the form on algae. However, judging by the shape of the intercostal pores illustrated by Norman (1903: pl. 9 fig. 5), his shell form was certainly not *P. gattyae*. Grant & Hayward (1986) recorded *P. gattyae* on shells from the English Channel, but the species has not been found on re-examination of their material. It would appear that their records of *P. gattyae* refer largely to material of *P. modica* n.sp. Other material on shell substrates in the collections of the BMNH originally registered under the name *gattyae* has been incorrectly identified with one exception, 1911.10.1.735A; the remainder comprises *P. arrecta* n.sp., *P. bifida, P. corbula* n.sp. and, most commonly, *P. modica* n.sp.

P. gattyae has been widely reported in the Mediterranean, including the Adriatic and Aegean Seas. It is known from SW. England and the Channel Islands. The most northerly records that could be substantiated were both on shell, from Galway (BMNH 1899.5.1.717) and Belfast (BMNH 1911.10.1.735A).

Puellina (Puellina) setosa (Waters, 1899)

(Figs 11–19 and Table 3)

not *Cribrilina radiata* var. α Hincks, 1880; 186, 190 (= *Puellina modica* n.sp.).
not *Cribrilina radiata* 'with vibraculoid setae': Hincks, 1880; pl. 25 fig. 5 (= *Puellina innominata*).
Cribrilina setosa Waters, 1899; 8, 9.
not *Puellina setosa*: Osburn, 1950; 186, pl. 29 fig. 4.
Puellina setosa: Harmelin, 1968; 1196, 1198, fig. 3(3, 4).
not *Cribrilaria setosa*: Harmelin, 1970; part 88–91, fig. 1m, pl. 2 figs 4, 5 (= *C. cassidainsis* Harmelin, 1984).
not *Cribrilaria setosa*: Harmelin, 1978; 189 (= *C. cassidainsis* Harmelin, 1984).
Puellina setosa: Hayward & Ryland, 1979; 68, fig. 19A–D.
Puellina setosa: Harmelin, 1984; 81–82, 85–87, figs 1, 5, 6, 14.

MATERIAL EXAMINED BY SEM.

Lectotype (selected here): MM 1173 (Madeira, the colony occupying an extensive section of the upper margin of the shell fragment and touching a balanid barnacle near the right (narrower) end of the substrate, viewed with the microslide's labels the correct way up).

BMNH: 1911.10.1.727a–c (Fosse de Cap Breton, colonies on stone).

MM: 1173 (Madeira, two paralectotype colonies on same shell as lectotype); 1137 (Naples, three colonies on alga).

OTHER MATERIAL.

BMNH: 1911.10.1.727 (Fosse de Cap Breton, several colonies on stone).

MM: 1173 (Madeira, one paralectotype colony on same shell as lectotype); 989 and 1006 (Naples, both labelled *gattyae*).

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material multiserial, with several hundred autozooids. Autozooid of variable shape in frontal view, generally sub-oval (longer than broad), occasionally proximally bifid. Gymnocyst of autozooid narrow distolaterally, of moderate width proximolaterally, and broad proximally, with proximal extension(s) between neighbouring zooids; gymnocyst often with fine radial striations.

Frontal shield (= pericyst) generally almost circular in outline, moderately calcified, with little or no differential median thickening, with 7–12 costae (usually 9 or 10). Each costa with broad, very short, moderately ascending basal portion at periphery of frontal shield leading to tapering, nearly horizontal subsequent portion contributing to slightly convex central region of shield.

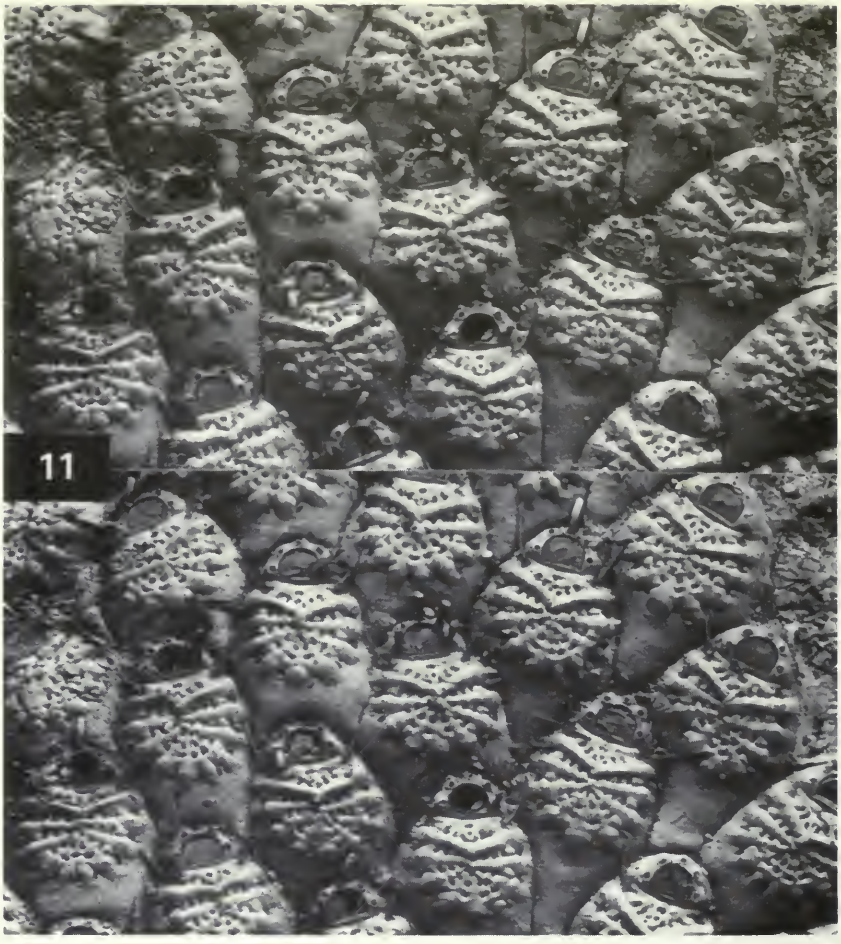
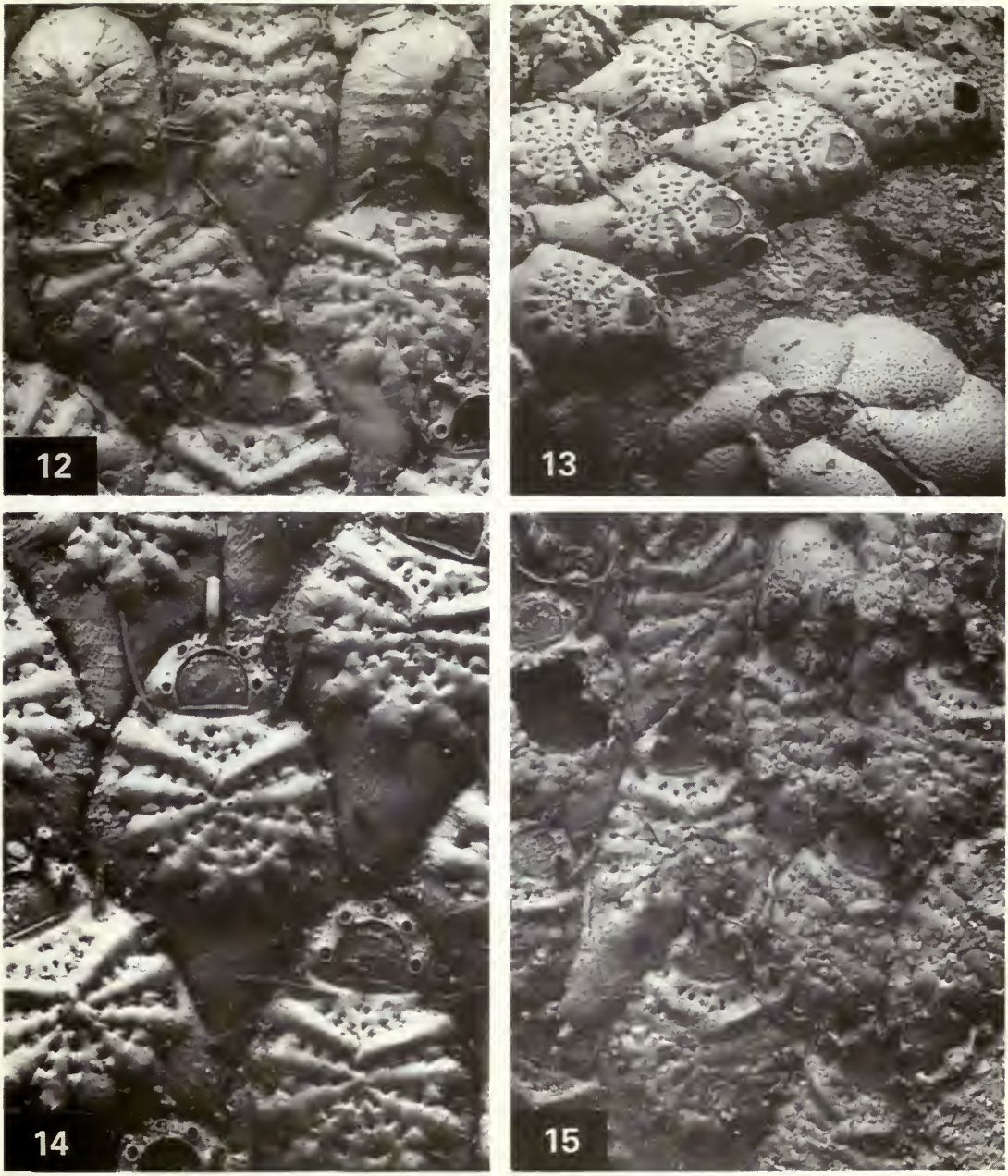


Fig. 11 *Puellina setosa* (Waters): stereo pair of BMNH 1911.10.1.727c, Fosse de Cap Breton, × 73.

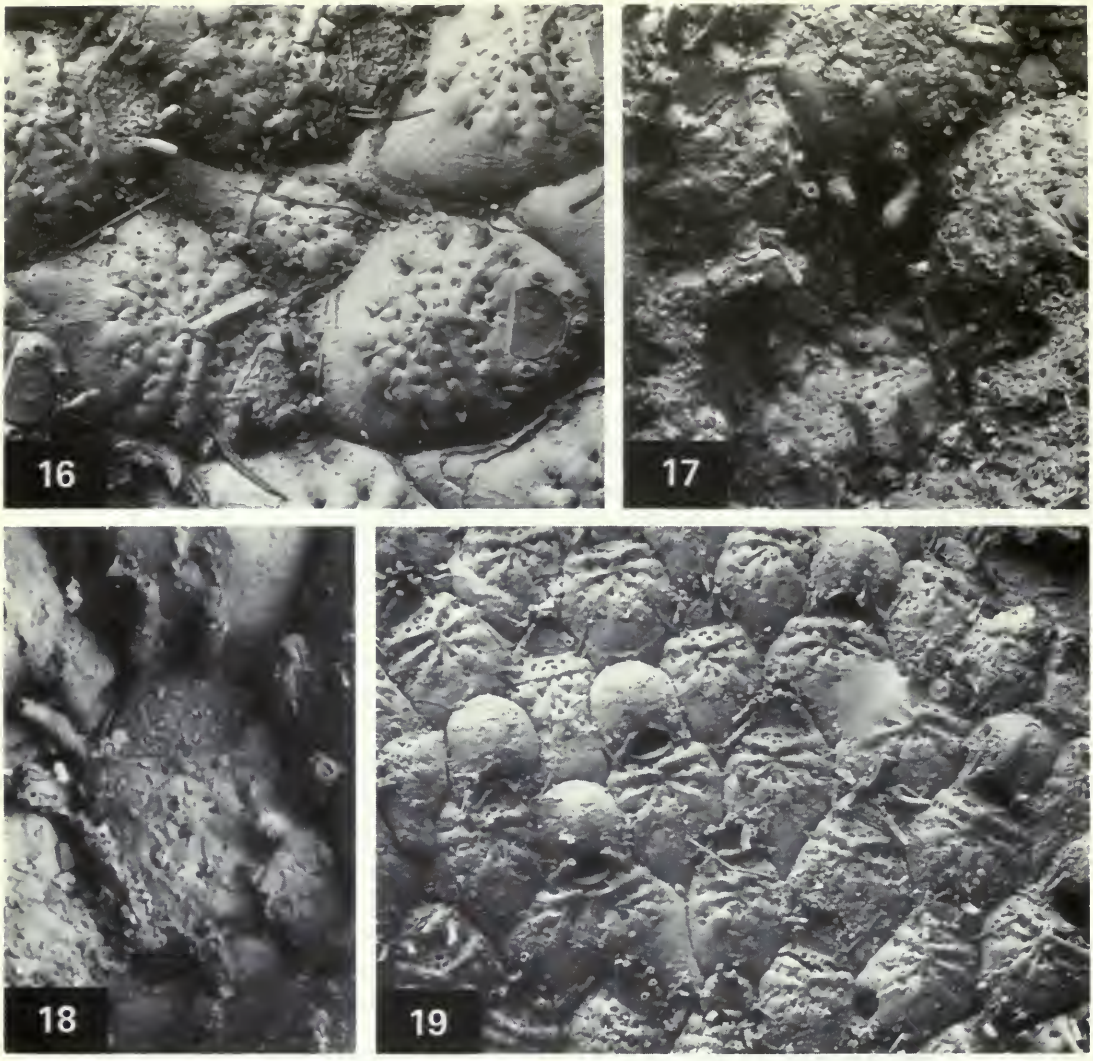
Costae without distinct ornamentation; first pair slightly prominent (sometimes forming very small median umbo), remainder low. Each costa frequently with pelmatidium near centre of shield and smaller pelmatidium near base. Intercostal pores sub-rectangular or reniform, relatively uniform in size throughout shield, often with denticle (sometimes 2) adjacent to intercostal suture; usually 2 or 3, occasionally 4, pores between successive costae. Lipped papilla pore between successive costae, about same size as adjacent intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, slightly broader than long, proximal edge straight. Orifice of ovicellate zooid not appearing truncate in frontal view; width 1·2–1·3 times that of orifice of non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 2 in ovicellate zooid; with brown chitinous joint at base but without subsequent segmentation, without apophyses. Apertural bar sloping slightly upwards from proximal margin of orifice to first row of intercostal pores, with pelmatidium on either side of median suture; without tubercles. Median sub-oral lacuna, about same size as an intercostal pore, frequently with denticle (occasionally 2) on proximal margin; one colony, BMNH 1911.10.1.727c, frequently with second, smaller median lacuna proximal to first lacuna and immediately distal to first row of intercostal pores.

Each autozooid with *c.* 8 distolateral pore chambers; uncalcified external windows of pore



Figs 12–15 *Puellina setosa* (Waters): (12) ovicellate autozooids, BMNH 1911.10.1.727b, Fosse de Cap Breton, × 127; (13) edge of colony viewed at angle, BMNH 1911.10.1.727c, Fosse de Cap Breton × 70; (14) non-ovicellate autozooid, same colony, × 144; (15) ovicellate and non-ovicellat autozooids, lectotype (MM 1173), Madeira, × 101.



Figs 16–19 *Puellina setosa* (Waters): (16) kenozooid and non-ovicellate autozooids, BMNH 1911.10.1.727b, Fosse de Cap Breton, × 125; (17) ancestrula (distal end faces bottom left), paralectotype (MM 1173), Madeira, × 190; (18) ancestrula regenerated as autozooid, lectotype (MM 1173), Madeira, × 290; (19) ovicellate and non-ovicellate autozooids, MM 1137, Naples, × 60.

chambers (seen in zooids on edge of colony: Fig. 13) relatively small (only slightly larger than an intercostal pore).

Ovicell of category C (p. 4), length 0·8–1·0 times that of frontal shield of autozooid (sometimes 1·1 times in MM 1137, Naples); frontal surface punctate, frequently with very low median ridge, without discernible median suture.

Avicularium not present in available material.

Kenozooid (Fig. 16) infrequent, of variable size and shape, with cribrimorph frontal shield of costae in radiating pattern.

Ancestrula (Fig. 17) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Details of jointing (if any) of

spines not seen. Median proximal spine broad near tip. Spines without inwardly directed (or other) apophyses. Ancestrula sometimes regenerated as small autozooid (BMNH 1911.10.1.727a and lectotype: Fig. 18) which may lack oral spines, or sometimes as kenozooid (MM 1137, largest colony).

REMARKS. When Waters (1899) introduced the name *Cribrilina setosa*, he included only *Cribrilina radiata* var. α Hincks (1880) in the synonymy of the new species. It is therefore apparent that the specific name *setosa* was intended to replace Hincks' appelation var. α. However, there is no suggestion in Waters' unillustrated account that he actually examined material considered by Hincks to belong to var. α, and no specimen labelled *C. radiata* var. α is to be found amongst Hincks' material in the BMNH. The only indication concerning material available to Waters is as follows (1899:8): 'From an examination of specimens from Madeira and Naples, I cannot agree in calling this form with vibraculae a variety of *radiata*.' No type material of *Cribrilina setosa* seems to have been formally recognised by later authors. The Madeiran collection which formed the main subject matter for Waters' paper was stated (1899:7) to have been sent by J. Y. Johnson. Microslide MM 1173 is labelled in Waters' hand as follows: 'Cribrilina setosa. Waters. Madeira. J.Y.J.'s coll. ovicell 0·24 & Crib. Balzaci no suboral pore'. There is thus little doubt that this was part of the material described by Waters, even though there is no reference to the publication and no designation as type material on the labels. (A section on *Cribrilina balzaci* followed that on *C. setosa* in

Table 3 *Puellina setosa* (Waters): measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	48–58	53·3	6·28	10	Lf	150–237	196	11·1	21
b		52–58	56·3	4·17	6		160–235	197	11·9	14
c		56–58	56·6	1·66	5		157–173	167	4·01	6
d		54–59	56·6	3·48	7		143–191	170	7·71	19
e		58–64	61·1	4·31	7		180–238	202	9·30	10
f		54–60	57·4	3·78	10		177–206	191	4·54	16
a	lo	56–70	62·5	5·67	13	Lfg	201–367	280	15·4	21
b		58–66	63·3	5·83	8		242–397	301	14·2	12
c		62–73	67·4	6·67	5		294–324	308	4·65	5
d		71–78	74·6	4·63	5		266–347	305	7·66	18
e		62–78	71·6	7·34	8		242–374	318	14·8	8
f		69–75	71·8	3·61	10		272–418	328	11·3	16
a	loo	—	—	—	0	lf	140–207	181	11·3	21
b		77	—	—	1		170–216	192	9·36	8
c		—	—	—	0		146–167	154	4·71	8
d		93–99	97·0	3·10	4		154–269	190	15·3	18
e		94–96	95·0	1·68	2		162–220	188	9·12	10
f		—	—	—	0		177–199	190	3·29	17
a	Lov	—	—	—	0	lov	—	—	—	0
b		125–158	150	9·93	5		177	—	—	1
c		—	—	—	0		—	—	—	0
d		157–183	171	5·57	7		190–200	196	2·46	7
e		174–181	178	3·14	2		172–176	174	1·83	2
f		—	—	—	0		—	—	—	0

a = lectotype (MM 1173); b = paralectotype (MM 1173); c and d = MM 1137 (2 colonies); e = BMNH 1911.10.1.727b; f = BMNH 1911.10.1.727c.

Waters' paper.) Microslide MM 1137 is labelled in Waters' hand: 'Cribrilina ['setosa Wat.' crossed out] ['Gattyae' crossed out] Off Nisida Naples. 30 metres 30/10/['87' crossed out]79 5 spines without lateral avicularia or vibracula *radiata*'. There is therefore less evidence to connect this microslide directly with Waters' account, and Waters was apparently unsure of the identity of his Mediterranean material (which is nevertheless considered here to be conspecific with MM 1173 from Madeira). No other material labelled *setosa* has been located in the Waters Collection. Accordingly, the lectotype (Figs 15, 18) has been selected from the colonies on MM 1173.

Waters' material (MM 1173 and 1137, including the lectotype) is not in fact considered to be the species named *Cribrilina radiata* var. α by Hincks (1880:186). The number of costae on the frontal shield of the material from Madeira and Naples clearly exceeds that specified in Hincks' account, the arrangement of costae does not recall that described by the earlier author, and the ovicell of *Puellina setosa* does not bear nodular projections. Hincks' variety is considered to be the form named *Puellina modica* n.sp. below (see the Remarks on that species).

Osburn (1950) referred *Cribrilina setosa* to *Puellina*. Soule (1959) noted that at least part of Osburn's material had vicarious avicularia. The identity of the Pacific form with the specimens described by Waters is at best extremely doubtful, but Osburn's generic assignation is nevertheless correct with respect to Waters' material.

The illustrations of *P. setosa* by Hayward & Ryland (1979: fig. 19) are of BMNH 1911.10.1.727. The ancestrula they figured (1979: fig. 19D) has in fact regenerated as an autozooid, as suggested by Harmelin (1984) and Aristegui (1984). A similar regeneration in the lectotype is illustrated in the present paper (Fig. 18).

As noted by Waters (1899), *P. setosa* is very similar to *P. gattyae*. *P. setosa* may be distinguished from *P. gattyae* by the presence of more than 1 intercostal pore between successive costae; by the sub-rectangular or reniform shape of the intercostal pores, which have denticles (cf. rounded, without denticles); by the absence in all zooids of a well developed median umbo; and by the relatively less extensive proximal gymnocyst. Furthermore, the most distal pair of costae are slightly more prominent than the rest in *P. setosa*, a pattern not seen in *P. gattyae*.

In the Mediterranean, well documented records of *P. setosa* exist from the French coast, Naples, the Sicilian Channel and Greece (Waters, 1899; Harmelin, 1968; 1984). The species was recorded from Madeira by Waters (1899) and from the Canaries by Aristegui (1984). Having discounted *Cribrilina radiata* var. α Hincks, 1880 (see above), the most northerly Atlantic record for *P. setosa* that could be substantiated was from Fosse (= Gouf) de Cap Breton in the southern part of the Bay of Biscay (BMNH 1911.10.1.727). In view of the uncertainty that has surrounded the identity of the species, the record from the Irish Sea near the Isle of Man by Eggleston (1969) must be regarded as extremely doubtful. There seems to be no real evidence that the species occurs in British or adjacent waters.

Puellina (Puellina) modica n.sp.

(Figs 20–28 and Table 4)

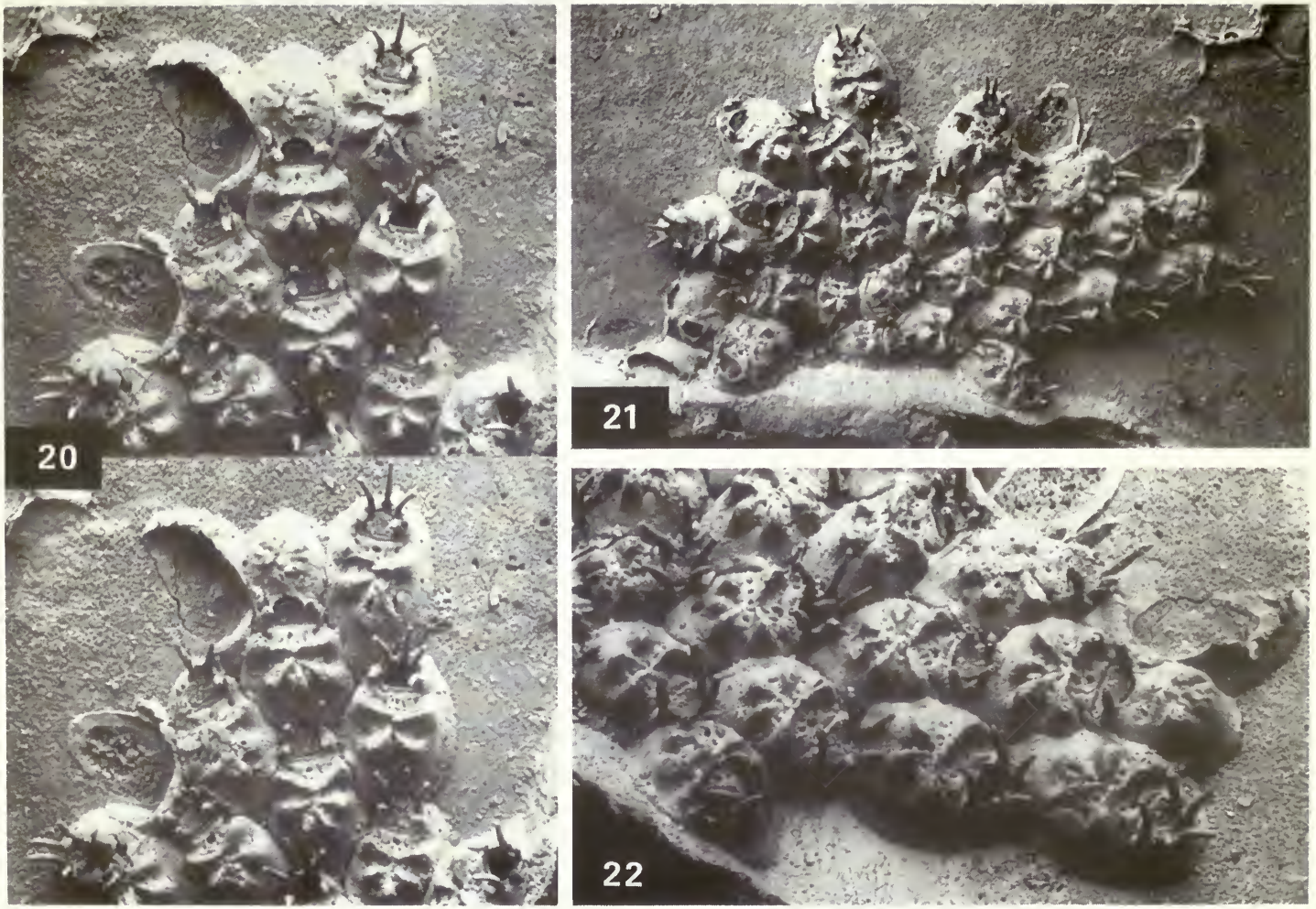
Lepralia innominata: Busk, 1854; pl. 86 fig. 3 (= BMNH 1847.9.16.79).
Cribrilina radiata var. α Hincks, 1880; 186, 190.
not *Cribrilina radiata* 'with vibraculoid setae': Hincks, 1880; pl. 25 fig. 5 (= *P. innominata*).

Holotype: BMNH 1985.11.20.58 (Channel Stn 249, 49°05·1′N 03°13·5′W, 77 m).

Paratypes (examined by SEM): BMNH: 1847.9.16.79 (British); 1936.12.30.331C (no locality [probably Liverpool Bay]); 1936.12.30.335A–C (Liverpool Bay); 1985.11.20.46 (Channel Stn 230); 1985.11.20.69i and 1985.11.20.71b,c (Channel Stn 252); 1985.11.20.106a,b (Channel Stn 275); 1985.11.20.112b (Channel Stn 315).

OTHER MATERIAL.

BMNH: 1847.9.16.139 and 1847.9.18.66 (British); 1899.5.1.1028 (Antrim, colony on shell A); 1899.5.1.1089 (Antrim, colony on shell A); 1899.5.1.1387 (Antrim, deep water); 1911.10.1.737C,D (Guernsey); 1936.12.30.329A–C (Isle of Man); 1963.2.12.349 (Hastings); 1985.11.20.50b,c and 1985.11.20.51 (Channel Stn 247); 1985.11.20.52f and 1985.11.20.54h (Channel Stn 248); 1985.11.20.55 and 1985.11.20.57c (Channel Stn 249); 1985.11.20.60b, 1985.11.20.61b, 1985.11.20.63c and 1985.11.20.64i–m (Channel Stn 250);



Figs 20–22 *Puellina modica* n.sp., holotype (BMNH 1985.11.20.58), Channel Stn 249: (20) stereo pair, × 75; (21) whole colony, × 51; (22) edge of colony viewed at angle, × 100.

1985.11.20.65b, 1985.11.20.66 and 1985.11.20.67c (Channel Stn 251); 1985.11.20.69j–m, 1985.11.20.70b–d, 1985.11.20.71d and 1985.11.20.72l (Channel Stn 252); 1985.11.20.85b, 1985.11.20.87c,d and 1985.11.20.88c–h (Channel Stn 257); 1985.11.20.91c–h, 1985.11.20.92b, 1985.11.20.93b, 1985.11.20.94e, 1985.11.20.95a–e, 1985.11.20.96b,c and 1985.11.20.98c (Channel Stn 258); 1985.11.20.100d (Channel Stn 260); 1985.11.20.104i (Channel Stn 263); 1985.11.20.105h,i and 1985.11.20.106c,d (Channel Stn 275); 1985.11.20.108e,f (Channel Stn 314); 1985.11.20.115 (Channel Stn 317); 1985.11.20.116l (Channel Stn 318).

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material pluriserial to multiserial, with over 100 autozooids. Autozooid of variable shape in frontal view, generally round or sub-oval (longer than broad). Lateral gymnocyst of autozooid of moderate width or broad; proximal gymnocyst broad, frequently with short proximal extension(s) between neighbouring zooids; gymnocyst often with fine radial striations.

Frontal shield (= pericyst) generally almost circular in outline, moderately to heavily calcified, with little or no differential median thickening and no umbo, slightly convex, with 4–6 (most commonly 5) short tapering costae converging towards single point on midline. Each costa without clearly differentiated basal and subsequent portions; costal ridge, with longitudinal crest, occupying almost entire length of costa and generally decreasing gradually in height from periphery to centre of shield; without tubercles. Most distal pair of costae forming very shallow V in frontal view, with their costal ridges sometimes continuous from side to side. Intercostal pores subrectangular or reniform, small, relatively uniform in size throughout shield, often with denticles adjacent to intercostal suture; 1 or 2 pores between successive costae. Lipped papilla pore between bases of successive costae, larger than adjacent intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, slightly broader than long, proximal edge straight. Orifice of ovicellate zooid not appearing truncate in frontal view; width 1·1–1·2 times that of orifice of non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 2 in ovicellate zooid; with brown chitinous joint at base but without subsequent segmentation, slightly curved or straight, without apophyses. Apertural bar without marked proximal-distal slope; frequently with minute pelmatidium on each side of median suture; without tubercles. (Pelmatidia not observed elsewhere on shield.) Single, large, median sub-oral lacuna (Fig. 24), considerably larger than an intercostal pore, frequently with pair of denticles on proximal margin.

Each autozooid with 5–8 lateral and distolateral pore chambers; uncalcified external windows of pore chambers, seen in zooids on edge of colony, relatively small (slightly smaller than sub-oral lacuna).

Ovicell of category C (p. 4), length 1·2–1·5 times that of frontal shield of autozooid; frontal surface punctate, uncalcified spots being borne on *c.* 5 indistinct ridges in more or less radiating pattern or on tubercles; median suture occasionally discernible.

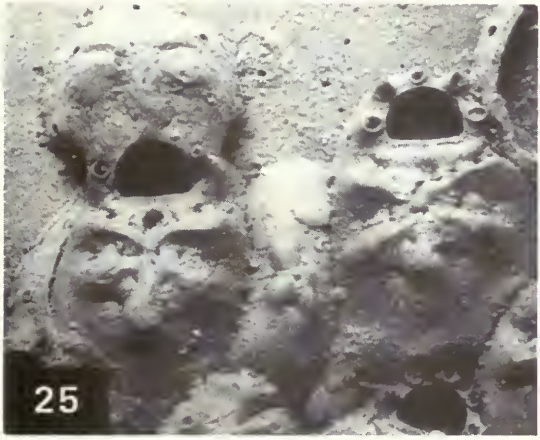
Avicularium not present in available material.

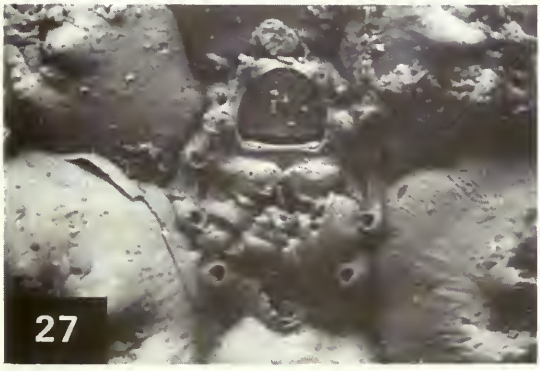
Kenozooid (Fig. 25) infrequent; single example seen, smaller than an autozooid, with rudimentary cribrimorph frontal shield of costae in more or less radiating pattern.

Ancestrula (Figs 26, 28) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Erect spines jointed at base; subsequent segmentation not observed. Median proximal spine tapering towards tip (not bifid). Spines without apophyses. Ancestrula sometimes regenerated as autozooid (Fig. 27) or kenozooid.

ETYMOLOGY. L. *modicus*—not very large, humble; referring to the modest size of both zooids and colonies of this species.

REMARKS. In addition to the *radiata* and *innominata* forms, Hincks (1880) included three varieties, α, β and γ, in his concept of *Cribrilina radiata*. *Cribrilina radiata* var. α was originally characterised (Hincks, 1880: 186) by its very small zooids, each with 5 very prominent costae on the frontal shield; the distal pair of costae formed a 'wall' proximal to the orifice; the ovicell bore nodular projections. Hincks also mentioned the presence of two slender vibraculoid setae (i.e. setiform papillae) in var. α, and this observation alone was taken to characterise the taxon by subsequent workers. Hincks made no reference to any particular figure in his account. Nevertheless a number of later authors seem to have taken Hincks' plate 25 figure 5 to depict var. α, although only





Figs 23–28 *Puellina modica* n.sp.: (23) ovicellate and non-ovicellate autozooids at edge of colony, BMNH 1985.11.20.71c, Channel Stn 252, ×97; (24) distal part of non-ovicellate autozooid, same specimen, ×310; (25) kenozooid, ovicellate and non-ovicellate autozooids, BMNH 1985.11.20.106a, Channel Stn 275, ×148; (26) ancestrula, holotype (BMNH 1985.11.20.58), Channel Stn 249, ×250; (27) ancestrula regenerated as autozooid, BMNH 1985.11.20.46, Channel Stn 230, ×250; (28) ancestrula, BMNH 1985.11.20.69i, Channel Stn 252, ×181.

Table 4 *Puellina modica* n.sp.: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	42–55	47·6	8·17	9	Lf	111–148	125	9·70	12
b		48–57	52·9	5·41	15		108–149	127	8·92	21
c		46–52	48·0	6·19	5		111–136	124	8·76	5
d		47–49	48·0	1·54	5		104–137	120	6·93	16
a	lo	53–60	56·3	4·13	8	Lfg	178–272	229	13·6	12
b		56–65	59·9	4·92	17		192–319	234	12·7	20
c		57–64	60·6	4·68	5		171–226	202	12·5	5
d		59–64	61·7	4·42	3		177–247	203	9·82	16
a	loo	61–69	65·0	9·79	2	lf	89–118	105	8·44	12
b		69–72	69·6	2·03	5		93–124	105	8·17	20
c		—	—	—	0		89–106	100	7·23	5
d		70	70·0	0·00	2		84–113	101	8·82	13
a	Lov	137–141	139	2·30	2	lov	141–151	146	5·45	2
b		140–158	147	5·57	4		173–200	183	6·73	5
c		—	—	—	0		—	—	—	0
d		137–151	143	4·81	4		135–167	153	8·66	5

a = holotype (BMNH 1985.11.20.58); b = BMNH 1847.9.16.79; c = 1936.12.30.335B; d = BMNH 1985.11.20.71c.

Hayward & Ryland (1979) categorically stated this interpretation of the figure, while Prenant & Bobin (1966) seemed to attribute a similar opinion to Osburn (1950). The figure was apparently assumed to portray var. α because the legend stated [*Cribrilina radiata*] 'with vibraculoid setae'. Waters (1899) introduced the name *Cribrilina setosa* with the apparent intention of elevating *Cribrilina radiata* var. α Hincks, 1880 to specific rank. The name *setosa* has accordingly been used subsequent to its introduction for material considered to resemble Hincks' plate 25 figure 5 and with conspicuous setiform papillae.

The interpretation of Hincks' plate 25 figure 5 as a depiction of *Cribrilina radiata* var. α in the sense of Hincks (1880) is not accepted here. As was noted by Hayward & Ryland (1979), the greater number and different disposition of costae in the figure are clearly at variance with Hincks' written account of the variety. The figure is in fact probably of *Puellina innominata*, an opinion shared by Harmelin (1970:85). Nor is var. α considered to be *Puellina setosa* as defined by the lectotype of *P. setosa* chosen above from Waters' material. Rather, Hincks' account is thought to have referred to *Puellina modica* n.sp., with which it agrees closely.

It is not entirely clear whether Hincks regarded the 'vibraculoid setae' as unique to var. α. These structures are referred to elsewhere in his (Hincks, 1880) general account of *C. radiata*: p. 186 ('orifice semicircular, . . . on each side of it a very delicate setiform appendage, often wanting') and p. 189 ('The small vibraculoid appendages are often wanting'). They are indeed shown by him in plate 25 figure 2, in the '*innominata* form'. However, Hincks (1883:443) later referred to 'the form which bears vibraculoid setae' in a way which implied that he did consider that these structures characterised a single form or variety within his concept of *C. radiata*. In fact setiform papillae occur throughout the subgenera *Puellina* and *Cribrilaria* as defined above.

Hincks (1880:190) indicated the provenance of his var. α material as 'Antrim, deep water (Hyndman)'. No specimen labelled *C. radiata* var. α has been found amongst Hincks' material in the BMNH. However, *P. modica* is to be found on a number of shells and stones (bearing other encrusting species and labelled with their names) from Antrim in the Hincks collection (e.g.

BMNH 1899.5.1.1028 and 1899.5.1.1089). In particular, a colony of the species occurred on (but has since been accidentally detached from) a stone encrusted by the cyclostome *Stomatoporina incurvata* (Hincks, 1859) which forms part of the type series (BMNH 1899.5.1.1387) of the cyclostome and is clearly documented as material provided by Hyndman from deep water off Antrim. There seems little doubt that *P. modica* is the form intended by Hincks as *C. radiata* var. α.

Puellina modica may be distinguished from its close relatives *P. gattyae* and *P. setosa* by its prominent costal ridges. Furthermore, each autozooid has relatively few (typically 5) costae, and the ovicell of *P. modica* has distinct ridges or tubercles whereas those of *P. gattyae* and *P. setosa* are almost smooth.

P. modica is also very similar to *P. rarecostata* (Reuss, 1848) from the Badenian (Middle Miocene) of the Vienna Basin (material of *P. rarecostata* examined by SEM: two syntypes, both NMV 1848/38/76; BMNH D55591; all from Eisenstadt). However, *P. rarecostata* has less prominent costal ridges than *P. modica* and a smooth ovicell. The fossil species is in fact intermediate in appearance between *P. modica* and *P. setosa*. It is regarded as a member of the subgenus *Puellina* as defined above.

The occurrence in *P. modica, P. bifida* and *P. praecox* n.sp. of ridges or tubercles on the ovicell and of costal ridges that are higher towards the edge of the frontal shield, and the absence of a median umbo in each, impart a similar appearance to these three species. In *P. bifida* and *P. praecox*, however, the exposed gymnocyst is less extensive than in *P. modica*, and the frontal shield more elongate and with more numerous costae. In addition, the oral spine bases are not brown. Unlike *P. modica* and *P. praecox, P. bifida* has category A or B ovicells (p. 4).

P. modica is known from the English Channel off Sussex, Normandy, Brittany and Guernsey at depths (where known) of 38–106 m; from the Irish Sea; and 'off Antrim' (including material from 'deep water').

Puellina praecox n.sp.

(Figs 29–35 and Table 5)

Holotype: BMNH 1985.11.20.52e (Channel Stn 248, 49°08·1′N 03°02·3′W, 73 m).

Paratypes (examined by SEM): BMNH: 1911.10.1.1182A (off Antrim); 1936.12.30.335A–C (Liverpool Bay); 1985.11.20.61a (Channel Stn 250); 1985.11.20.72h (Channel Stn 252); D55583 (Red Crag, Plio-Pleistocene, Walton-on-the-Naze, Essex); D55584, D55585, D55586a,b and D55587 (Red Crag, Plio-Pleistocene, Shottisham, Suffolk).

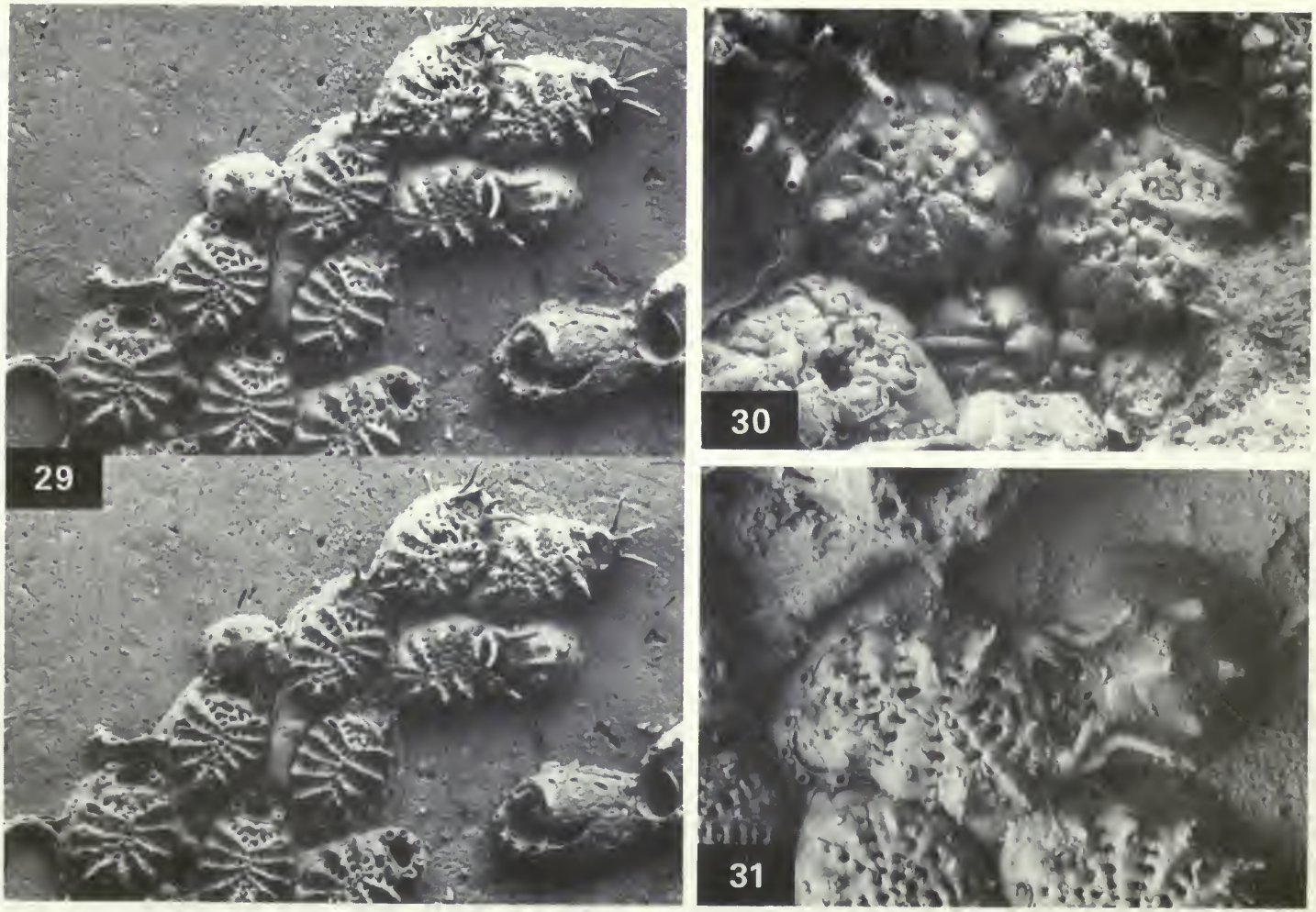
OTHER MATERIAL.

BMNH: 1936.12.30.332D (Liverpool Bay); 1936.12.30.333A (no locality [probably Liverpool Bay]); 1985.11.20.91i (Channel Stn 258).

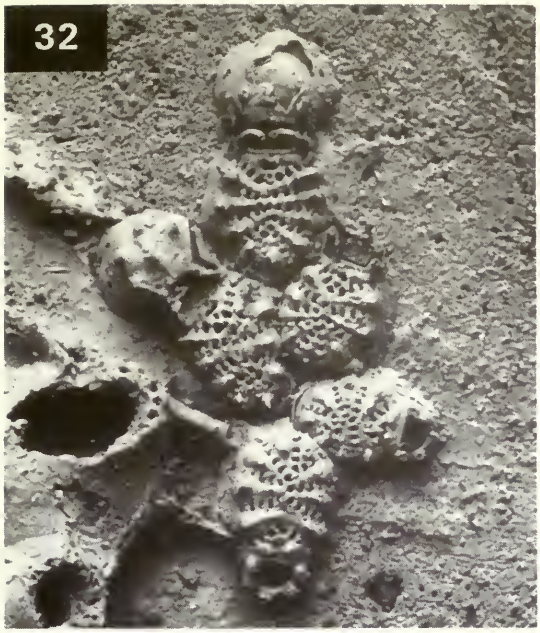
DESCRIPTION. Colony encrusting, unilaminar, minute, zooids distinct; largest colonies in available material pluriserial, with only *c.* 20 autozooids. Autozooid generally sub-oval in frontal view (longer than broad). Exposed lateral gymnocyst of autozooid narrow or absent (except at edge of colony); proximal gymnocyst narrow but occasionally with proximal extension(s) between neighbouring zooids.

Frontal shield (= pericyst) lightly calcified, without umbo or any other median thickening; with 8–10 costae each with short, broad, steeply ascending basal portion leading to tapering, nearly horizontal subsequent portion contributing to slightly convex central region of shield. Each costa generally with ridge, decreasing in height gradually from periphery to centre of shield, plus tubercle (occasionally with pelmatidium) near base; degree of development of ridge and tubercle variable. Intercostal pores of variable shape (circular, sub-oval, reniform or sub-rectangular), of variable size throughout shield but often larger in first intercostal row (i.e. just proximal to orifice) than elsewhere, sometimes with denticles adjacent to intercostal suture; 4 (occasionally 3) pores between adjacent costae. Lipped papilla pore between bases of successive costae, about size of adjacent intercostal pore.

Orifice of autozooid D-shaped, slightly broader than long, proximal edge straight. Orifice of ovicellate zooid not appearing truncate in frontal view; width 1·1–1·2 times that of orifice of



Figs 29–31 *Puellina praecox* n.sp.: (29) stereo pair of holotype (BMNH 1985.11.20.52e), Channel Stn 248, × 75; (30) ancestrula regenerated as kenozooid, with periancestrular non-ovicellate autozooids, BMNH 1985.11.20.61a, Channel Stn 250, × 250; (31) ovicellate autozooid (budded from periancestrular autozooids) part of which occupies zooecium of ancestrula (distal end of ancestrula faces bottom left), BMNH 1936.12.30.335C, Liverpool Bay, × 187.



Figs 32–35 *Puellina praecox* n.sp.: (32) whole colony, BMNH 1936.12.30.335C, Liverpool Bay, × 87; (33) ovicellate autozooid, same specimen, × 210; (34) ancestrula and periancestrular autozooids, BMNH 1936.12.30.335A, Liverpool Bay, × 183; (35) whole colony, BMNH D55586b, Red Crag (Plio-Pleistocene), Shottisham, Suffolk, × 100.

Table 5 *Puellina praecox* n.sp.: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	44–51	47·3	5·12	11	Lf	169–210	198	6·23	10
b		49–54	51·5	7·73	2		173–219	193	9·46	6
c		—	—	—	0		180	—	—	1
d		40–44	41·7	5·42	3		113–139	128	7·59	7
e		41–45	43·0	7·40	2		168–195	182	11·8	2
f		—	—	—	0		164–189	179	7·27	4
g		38	—	—	1		141–179	163	12·0	4
h		—	—	—	0		137–163	150	13·8	2
a	lo	53–59	56·6	3·83	11	Lfg	203–300	254	12·9	10
b		54–59	56·5	7·04	2		203–301	241	18·8	6
c		—	—	—	0		210	—	—	1
d		47–48	47·5	1·68	2		135–173	162	8·29	7
e		54–57	55·5	4·30	2		217–260	239	14·4	2
f		49–53	51·0	6·24	2		—	—	—	0
g		47	—	—	1		181–231	212	11·8	4
h		—	—	—	0		191–199	195	3·26	2
a	loo	63–72	67·5	10·6	2	lf	143–172	157	6·08	9
b		62–67	64·5	6·17	2		141–166	154	5·81	6
c		65–68	66·5	3·59	2		139–149	144	5·52	2
d		47–55	51·0	12·5	2		97–114	105	7·44	4
e		64	—	—	1		139–148	144	4·98	2
f		—	—	—	0		138–188	156	15·4	4
g		55	—	—	1		145–162	155	5·10	4
h		55	—	—	1		119–134	127	9·44	2
a	Lov	128–148	138	11·6	2	lov	154–167	161	6·45	2
b		130–173	149	12·9	4		160–193	180	9·00	4
c		135–138	137	1·74	2		187–193	190	2·51	2
d		119	—	—	1		124–147	134	9·41	3
e		118	—	—	1		145	—	—	1
f		155	—	—	1		230	—	—	1
g		158	—	—	1		180	—	—	1
h		—	—	—	0		—	—	—	0

a = holotype (BMNH 1985.11.20.52e); b = BMNH 1936.12.30.335A; c = BMNH 1936.12.30.335C; d = BMNH 1985.11.20.61a; e = BMNH 1911.10.1.1182A; f = BMNH D55586a; g = BMNH D55586b; h = BMNH D55584.

non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 4 in ovicellate zooid; jointed just above base but without subsequent segmentation, without apophyses. Apertural bar with low tubercle on each side of median suture, and pelmatidium on each tubercle. Median sub-oral lacuna larger than an intercostal pore, of variable shape, occasionally with denticles on proximal margin; occasionally a second lacuna proximal to main lacuna (Fig. 33), smaller than most intercostal pores, denticles not observed.

Each autozooid with *c.* 5 distolateral pore chambers; uncalcified external windows of pore chambers, seen in zooids on edge of colony, relatively small (about the size of an intercostal pore).

Ovicell of category C (p. 4), length 0·7–0·9 times that of frontal shield; frontal surface usually with 2–5 prominent tubercles, sometimes with uncalcified tops.

Kenozooid not present in available material.

Avicularium not present in available material.

Ancestrula (Fig. 34) tatiform, with median proximal spine plus 5 pairs of spines around edge of gymnocyst (i.e. total of 11 spines). Spine morphology unknown. Ancestrula sometimes regenerated as kenozooid (Fig. 30).

ETYMOLOGY. L. *praecox*—ripe before its time, premature, precocious; referring to the development of ovicells early in astogeny in this species.

REMARKS. The dimensions of BMNH 1985.11.20.61a were noticeably smaller than those of the other material measured (Table 5). However, no further differences were noted between this specimen and the others.

P. praecox n.sp. closely resembles *P. bifida*, especially in details of the frontal shield (including the apertural bar). However, the frontal shield of *P. praecox* is less heavily calcified than in *P. bifida*, with the costal ridges less well developed. The oral spines of *P. praecox* lack apophyses. The ovicell is of category C (p. 4) (cf. category A or B in *P. bifida*) and typically bears tubercles rather than ridges. The two species may occur at the same locality (Channel Stns 248, 250 and 252) and even on the same shell substrate (BMNH 1985.11.20.52 and 1985.11.20.72).

Puellina praecox would be a typical member of the subgenus *Cribrilaria* as defined above but for its category C ovicell. The absence of avicularia may be regarded as a correlate of the small colony size reached by this species.

P. praecox is known from the English Channel off Brittany at depths of 73–99 m; from the Irish Sea; from off Antrim; and as a fossil on shells from the Red Crag (Plio-Pleistocene) of Essex and Suffolk (North Sea basin).

***Puellina directa* n.sp.**

(Figs 36–42 and Table 6).

Holotype: BMNH 1985.11.20.76b (Channel Stn 253, 48°52·2′N 03°54·0′W, 79 m).

Paratypes (examined by SEM): BMNH: 1985.11.20.64e (Channel Stn 250); 1985.11.20.76c,d (Channel Stn 253); 1985.11.20.94d (Channel Stn 258); 1985.11.20.109c and 1985.11.20.110a (Channel Stn 314).

OTHER MATERIAL.

BMNH: 1985.11.20.54f,g (Channel Stn 248); 1985.11.20.56a,b and 1985.11.20.59h (Channel Stn 249); 1985.11.20.62 and 1985.11.20.64f,g (Channel Stn 250); 1985.11.20.65a and 1985.11.20.67b (Channel Stn 251); 1985.11.20.69e,f and 1985.11.20.72i,j (Channel Stn 252); 1985.11.20.83d–f (Channel Stn 256); 1985.11.20.90c,d and 1985.11.20.97b (Channel Stn 258); 1985.11.20.105e–g (Channel Stn 275); 1985.11.20.108g and 1985.11.20.110b (Channel Stn 314).

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material pluriserial to multiserial, with *c.* 100 autozooids. Autozooid of variable shape in frontal view, generally sub-oval (longer than broad). Lateral and proximal gymnocyst of autozooid broad, frequently with short proximal and proximo-lateral extensions between neighbouring zooids.

Frontal shield (= pericyst) moderately to heavily calcified, with little or no differential median thickening, strongly convex, with 7–10 costae (usually 7 or 8). Each costa without clearly differentiated basal and subsequent portions; costal ridge (with narrow longitudinal crest) occupying almost entire length of costa. Most distal two (occasionally three) pairs of costae usually almost parallel, with left and right members of each pair abutting on midline and forming straight line across shield; ridges of these distal costae especially prominent (with crest often irregularly serrate), sometimes continuous from one side of shield to other but more commonly interrupted by narrow V-shaped notch at midline (the latter arrangement especially noticeable when viewed obliquely: Fig. 38). Intercostal pores sub-rectangular or reniform, relatively uniform in size throughout shield, often with denticles adjacent to intercostal suture; usually 3 or 4 pores between successive costae, but frequently fewer between short proximal costae. Lipped papilla pore between bases of successive costae, about same size as, or slightly larger than, an intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, clearly broader than long, proximal edge straight. Orifice of ovicellate zooid not appearing truncate in frontal view; width *c.* 1·3 times that of orifice of

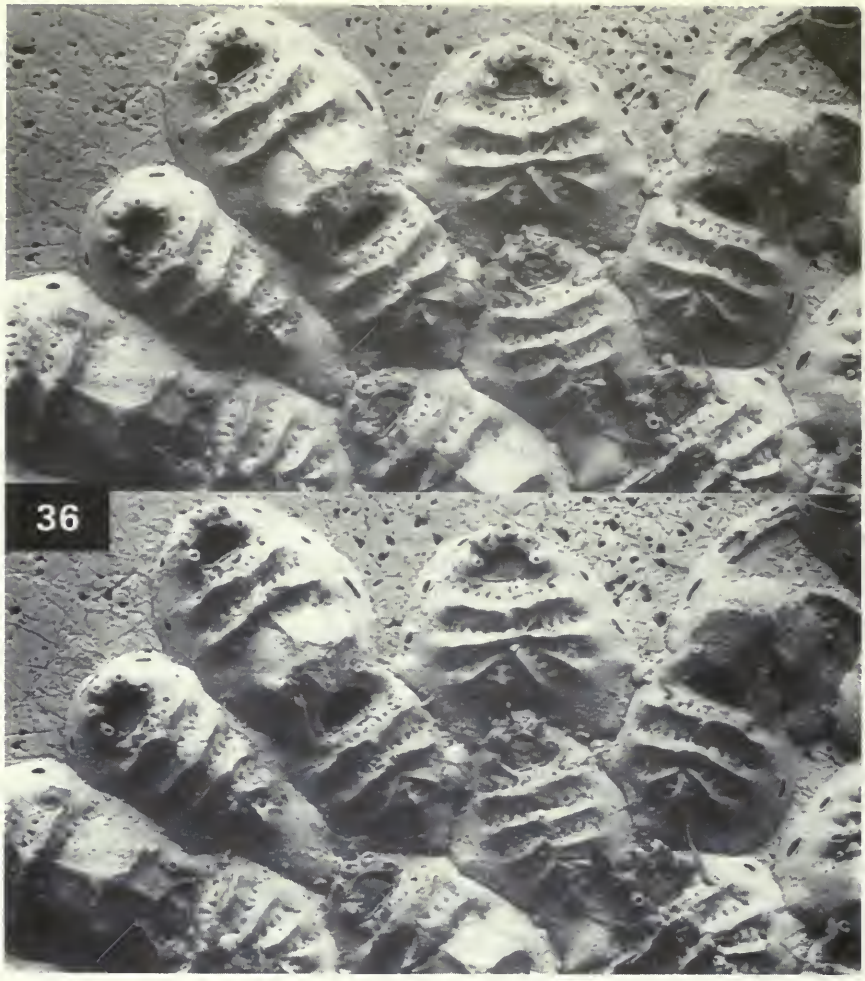


Fig. 36 *Puellina directa* n.sp.: stereo pair of BMNH 1985.11.20.110a, Channel Stn 314, × 103.

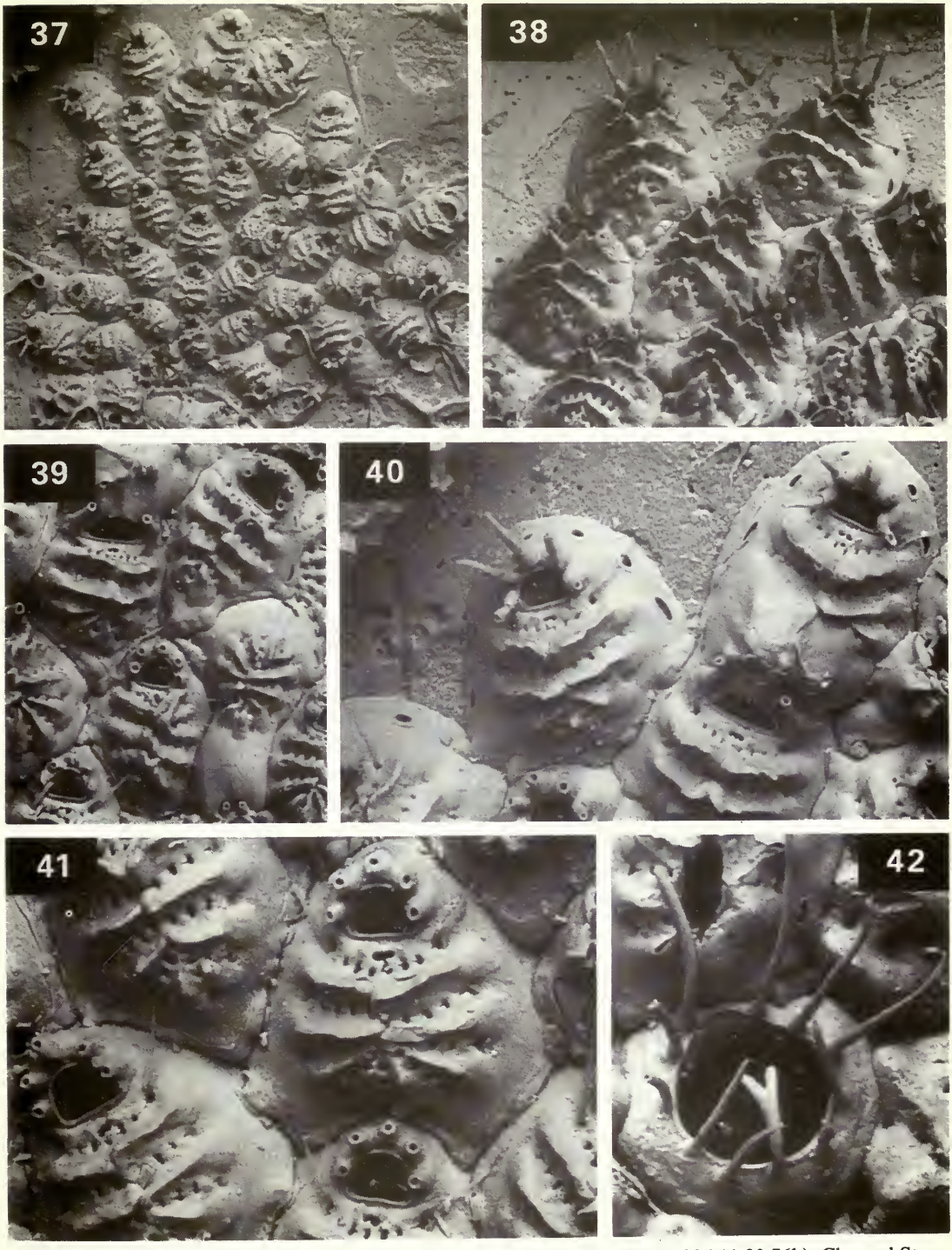
non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 2 in ovicellate zooid; jointed some distance above base (Fig. 38), without apophyses. Apertural bar sloping upwards from proximal margin of orifice to first row of intercostal pores; with tubercle each side of median lacuna; minute pelmatidium on each tubercle, and median suture, occasionally discernible. (Pelmatidia not seen elsewhere on shield.) Single median sub-oral lacuna larger than an intercostal pore, frequently with 1 or 2 denticles (which may subdivide lacuna) on proximal margin.

Each autozooid with 5–8 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony) of variable size, generally rather small but considerably larger than an intercostal pore.

Ovicell of category A (p. 4), length 0·7–1·1 (usually *c.* 0·9) times that of frontal shield of autozooid; frontal surface non-punctate, generally with median ridge (occasionally with concurrent suture) plus 1 or 2 shorter ridges on each side radiating from median ridge.

Avicularium not present in available material.

Kenozooid (Fig. 39) infrequent, up to size of autozooid, with cribrimorph frontal shield of costae in radiating pattern; gymnocyst broad.



Figs 37–42 *Puellina directa* n.sp.: (37) whole colony, holotype (BMNH 1985.11.20.76b), Channel Stn 253, ×38; (38) edge of colony viewed at angle, holotype, ×95; (39) kenozooid with ovicellate and non-ovicellate autozooids, BMNH 1985.11.20.76c, Channel Stn 253, ×97; (40) ovicellate and non-ovicellate autozooids at edge of colony, holotype, ×129; (41) non-ovicellate autozooid, holotype, ×182; (42) ancestrula, BMNH 1985.11.20.76d, Channel Stn 253, ×240.

Table 6 *Puellina directa* n.sp.: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	40–48	43·2	7·70	6	Lf	128–162	149	7·19	8
b		43–49	46·0	4·69	7		154–206	175	8·88	9
c		37–48	43·3	6·02	20		131–212	164	11·8	24
a	lo	51–60	55·6	5·88	7	Lfg	173–257	211	12·4	8
b		55–66	60·7	6·21	6		210–294	241	11·2	8
c		58–66	61·0	3·72	20		209–326	241	14·4	23
a	loo	—	—	—	0	lf	117–137	124	5·70	8
b		77–83	79·0	4·76	3		122–148	132	8·40	8
c		75–80	77·0	2·21	9		110–157	135	8·68	29
a	Lov	—	—	—	0	lov	—	—	—	0
b		166	166	0·00	2		225	—	—	1
c		128–157	140	7·37	9		151–198	175	9·47	9

a = holotype (BMNH 1985.11.20.76b); b = BMNH 1985.11.20.76c; c = BMNH 1985.11.20.110a.

Ancestrula (Fig. 42) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of slender erect spines around edge of gymnocyst (i.e. total of 11 spines). Median proximal spine with strongly bifid tip. Spines without apophyses. Regeneration of ancestrula not seen.

ETYMOLOGY. L. *directus*—set straight, arranged in a straight line; referring to the disposition of the more distal pairs of costae in this species.

REMARKS. *P. directa* n.sp. resembles members of the subgenus *Puellina* as defined above (*P. gattyae, P. setosa* and *P. modica* n.sp.), except that the ovicell is non-punctate and of category A (p. 4). The species is best characterised by the arrangement of the more distal pairs of costae in parallel or sub-parallel lines right across the strongly convex frontal shield, by the strong costal ridges which tend to be higher towards the centre of the shield, and by the broad gymnocyst which is about as wide laterally as proximally.

P. directa is known only from the English Channel off Normandy and Brittany, at depths of 38–99 m.

Puellina (Cribrilaria) venusta Canu & Bassler, 1925
(Figs 43–49, 99 and Table 7)

part *Cribrilina radiata, radiata* form: Hincks, 1880; 185–190, pl. 25 figs 3, ?6.
Puellina venusta Canu & Bassler, 1925; 22, pl. 2 fig. 5.
Cribrilaria crenulata Harmelin, 1970; 91–93, fig. 1i–k, pl. 2 figs 1–3.
Cribrilaria venusta: Harmelin, 1978; 180, 182, 184, pl. 2 figs 3–5.
Cribrilaria venusta: Hayward & Ryland, 1978; 146.
part or whole *Cribrilaria radiata*: Hayward & Ryland, 1979; 62, 63, fig. 16A,B.
Cribrilaria venusta: Hayward & Cook, 1983; 43, 45, fig. 11A.

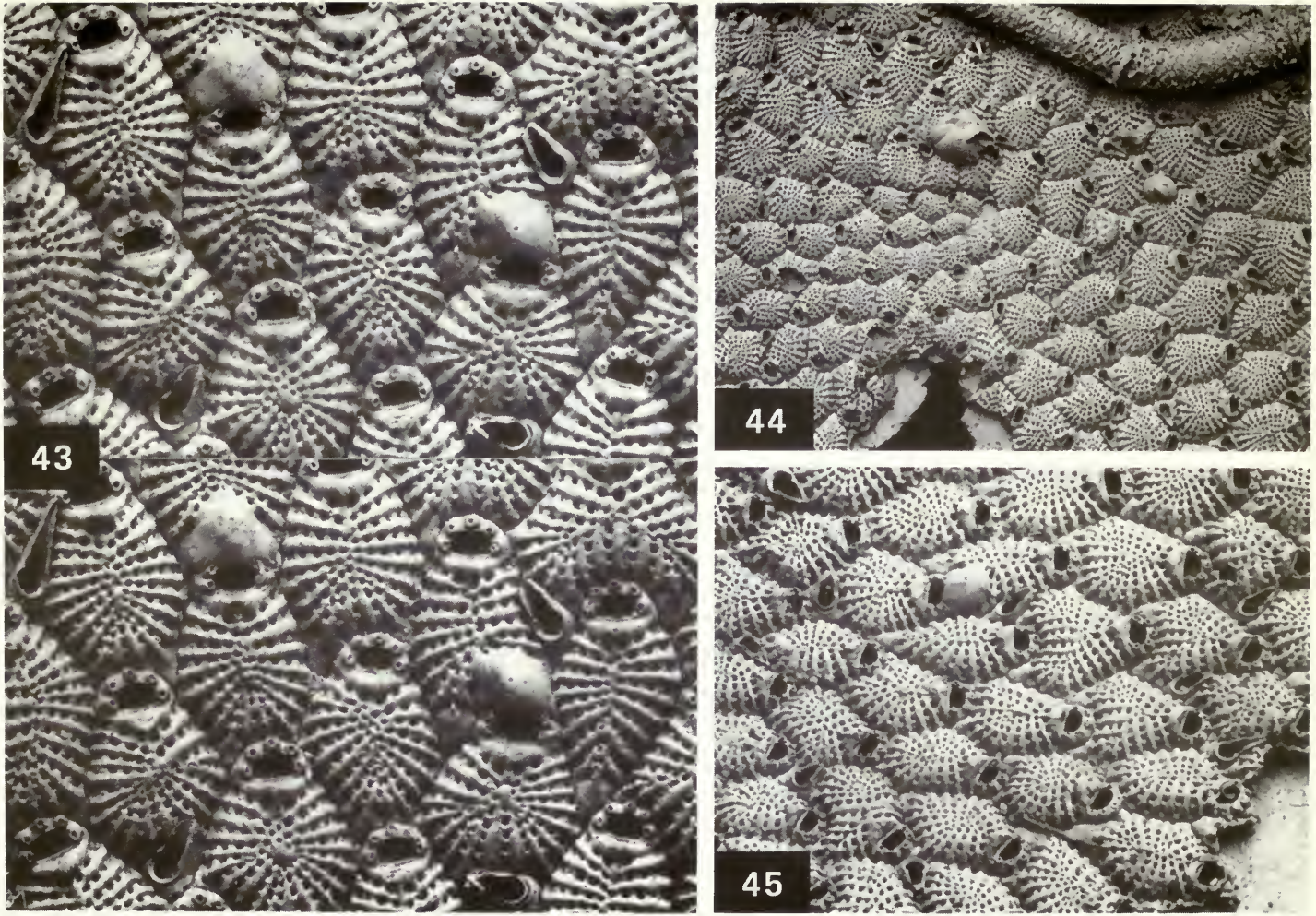
MATERIAL EXAMINED BY SEM.

BMNH: 1911.10.1.711 (Fosse de Cap Breton); 1985.11.20.68 (Channel Stn 252); 1985.11.20.82a (Channel Stn 256); 1985.11.20.117 (Channel Stn 318); D55588 (Badenian, Hartl-lucke, Eisenstadt).

LBIMM: BRY-6527 (Marseille, holotype of *Cribrilaria crenulata* Harmelin, 1970).

OTHER MATERIAL.

Holotype: IP, Canu Collection (no registration number) (34°12′N, 07°07′W, off Rabat, Morocco, 140–150 m).



Figs 43–45 *Puellina venusta* Canu & Bassler, BMNH 1985.11.20.82a, Channel Stn 256: (43) stereo pair, × 63; (44) colony origin and early generations of autozooids (all non-ovicellate), × 25; (45) part of colony viewed at angle. × 44.

BMNH: 1911.10.1.706 (Guernsey, two colonies on separate substrates); 1911.10.1.712 (Birturbuy [= Bertraghboy] Bay [Galway]); 1911.10.1.732 (Shetland, 320 m, colony and substrate, a pebble, broken in two); 1919.6.24.39 (Guernsey); 1985.1.2.54, 1985.1.2.83 and 1985.1.2.88 (northern Bay of Biscay); 1985.11.20.83b (Channel Stn 256); 1985.11.20.87b (Channel Stn 257); 1985.11.20.103b,c (Channel Stn 261); 1985.11.20.104c, d (Channel Stn 263); 1985.11.20.113 (Channel Stn 316).

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material multiserial, with well over 1000 autozooids. Autozooid of very variable shape in frontal view, generally sub-oval but commonly broadly bifid proximally (when passing to both sides of proximal zooid) or elongate. Exposed lateral and proximal gymnocyst of autozooid very narrow or absent (except at edge of colony), but frequently with short proximal extension(s) between neighbouring zooids.

Frontal shield (= pericyst) lightly to moderately calcified, without median thickening (except on apertural bar—see below), with 12–23 costae (most commonly 15–18; high numbers generally occurring in proximally bifid zooids, in which the pattern of costae may be partially duplicated, or in elongate zooids). Each costa with short, steeply ascending basal portion leading to tapering, nearly horizontal subsequent portion contributing to slightly convex central region of shield; without ornamentation; up to 3 minute pelmatidia along length of each costa. Intercostal pores sub-oval, of variable size throughout shield but generally slightly larger in row immediately proximal to apertural bar than in rest of shield, without denticles; 3 or 4 pores between successive costae. Lipped papilla pore between bases of successive costae, about size of adjacent intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, very clearly broader than long, proximal edge straight or indistinctly crenulate. Orifice of ovicellate zooid frequently appearing distally truncate to varying extent in frontal view because of overhanging calcification of ovicell; width 1·0–1·1 times that of orifice of non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 4 in ovicellate zooid; jointed just above base, with adjacent constriction (Fig. 47); apophyses not seen. Apertural bar forming short triangular area, sloping steeply upwards from proximal margin of orifice to form median sub-oral mucro; mucro of variable development, sometimes spiniform or bifid; apertural bar without tubercles; pelmatidia and median suture not seen. Without median sub-oral lacuna.

Each autozooid with about 9 distolateral pore chambers; uncalcified external windows of pore chambers, seen in zooids on edge of colony (Fig. 48), often sub-rectangular, very large (much larger than an intercostal pore).

Ovicell of category A (p. 4), with rather variable outline in frontal view, length 0·5–0·6 times that of frontal shield of autozooid; frontal surface non-punctate, with variably developed median or diagonal ridge, sometimes with concurrent suture.

Avicularium frequent, interzooidal, smaller than autozooid; palate elongate-triangular, inclined at low angle to substrate; rostrum generally directed between autozooids. Mandible equal in length to palate and of same shape, i.e. fitting into palate. Proximal gymnocyst short (much shorter than palate plus frontal non-calcified area).

Kenozooid (Fig. 48) infrequent, up to size of autozooid, with cribrimorph frontal shield of costae in radiating pattern.

Ancestrula (Fig. 49) tatiform, with median proximal spine plus 5 pairs of spines around edge of gymnocyst (i.e. total of 11 spines). Details of segmentation (if any) of spines not seen. Morphology of median proximal spine not seen. Other spines each with upwardly directed spiniform apophysis on inner surface near base. Regeneration of ancestrula not seen.

Figs 46–49 *Puellina venusta* Canu & Bassler: (46) ovicellate and non-ovicellate autozooids and avicularium, BMNH 1985.11.20.82a, Channel Stn 256, × 116; (47) non-ovicellate autozooids (some with basal portions of oral spines intact) and avicularia (with mandibles intact), BMNH 1985.11.20.68, Channel Stn 252, × 145; (48) edge of colony, maternal autozooid (top left) arrowed, BMNH 1911.10.1.711, Fosse de Cap Breton, × 49; (49) ancestrula, BMNH 1985.11.20.117, Channel Stn 318, × 230.

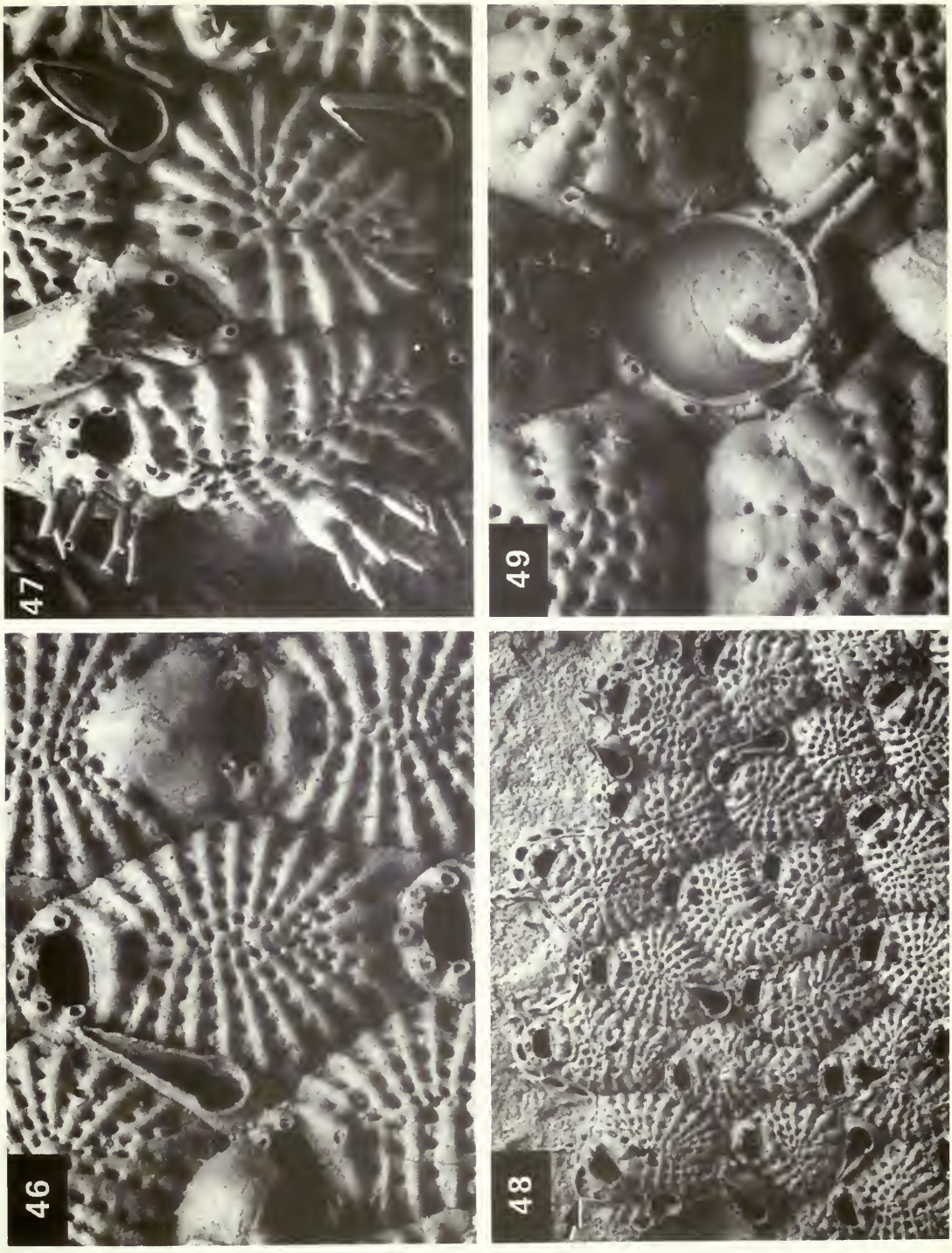

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Table 7 *Puellina venusta* Canu & Bassler: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	48–57	53·5	6·83	6	Lf	277–345	302	6·72	9
b		51–61	57·9	5·91	8		256–350	306	9·20	9
c		49–65	57·0	6·59	26		283–372	326	7·42	29
d		53–71	60·9	10·7	7		274–378	317	12·4	6
a	lo	80–95	85·1	6·64	7	Lfg	342–445	371	8·85	9
b		77–100	86·7	8·27	10		281–433	343	13·0	10
c		81–100	91·5	4·68	25		353–486	413	9·42	27
d		82–94	87·3	6·19	7		352–444	386	11·7	5
a	loo	87–94	90·3	4·21	3	lf	244–322	267	8·79	10
b		87	—	—	1		169–336	253	21·4	11
c		97	—	—	1		254–406	304	13·0	18
d		82–94	86·8	6·43	4		219–279	247	9·23	9
a	Lov	141–167	153	7·68	4	Lr	187–209	198	8·84	2
b		147	—	—	1		156	—	—	1
c		158–170	164	5·82	2		160–230	180	16·5	5
d		167–197	179	8·29	4		195–203	199	2·18	3
a	lov	152–168	163	6·15	3	Lav	220–241	231	7·25	2
b		155	—	—	1		233	—	—	1
c		184–228	206	17·0	2		183–284	221	18·4	5
d		195–213	207	4·37	4		220–245	231	6·06	3

a = BMNH 1911.10.1.711; b = BMNH 1985.11.20.68; c = BMNH 1985.11.20.82a; d = LBIMM-BRY-6527 (holotype of *Cribrilaria crenulata* Harmelin).

Remarks. In a taxonomic account of Mediterranean species referred to *Cribrilaria*, Harmelin (1970) redescribed *C. radiata* (Moll, 1803), of which a neotype was designated, and described as new a species to which he gave the name *C. crenulata*. *C. crenulata* was later realised (Harmelin, 1978) to be a geographical variant of the formerly overlooked species *Puellina venusta* Canu & Bassler, 1925, which had been described from the Atlantic off Morocco. The two forms *P. radiata* and *P. venusta* seem to be very closely related. *P. radiata*, as defined by the neotype, is thought to be restricted to the Mediterranean (Harmelin, 1978:174 and pers. comm. to JDDB, 1985), although the name has been widely applied to Atlantic material referable to *P. venusta*.

Traces of the crenulate proximal margin of the orifice shown by Mediterranean specimens described as *Cribrilaria crenulata* by Harmelin (1970) may be seen, albeit indistinctly, in some Atlantic material (BMNH 1911.10.1.711). As noted by Harmelin (1970), avicularia in Recent Mediterranean material frequently show multiple regenerations stacked one on top of the other; this was also reported in Atlantic material studied by Harmelin (1978) and Aristegui (1983). Autozooids of the holotype of *C. crenulata* have up to 12 distolateral pore chambers. Harmelin (1978:180) stated that oral spines of *P. venusta* sometimes have 'une couronne de spinules légèrement au-dessus de leur base'. The median proximal spine of the ancestrula of material studied by Harmelin (1970:92 and fig. 3b) has a bifid tip.

The specimen figured by Hayward & Ryland (1979: fig. 16A,B, as *Cribrilaria radiata*) is BMNH 1911.10.1.711 (Fig. 48). Part of the material studied by Hayward & Ryland (1978) is in the BMNH collections (1985.1.2.54, 1985.1.2.83 and 1985.1.2.88).

P. venusta is a common fossil species encrusting shells from the Badenian (Middle Miocene) of Eisenstadt in the Vienna Basin. The fossil (Fig. 99) has slightly more extensive gymnocyst than has most Recent material (Figs 43–49), but agreement is otherwise close. The Badenian of Eisenstadt is the type locality of a very similar species, *Puellina scripta* (Reuss, 1848). The holotype of *P. scripta*, NMV 1848/38/75, is illustrated in Figure 98, and is the only colony of the species examined. In this specimen the avicularium is consistently larger than in *P. venusta*, the sub-oral mucro of the autozooid is poorly developed or absent, and the frontal shield almost flat. *P. scripta* is therefore very close to the Recent Mediterranean species *P. radiata*. It differs only in the presence of 5 oral spines in all non-ovicellate autozooids whereas in *P. radiata* the usual complement is 4 spines, with 20–60% of zooids in rare colonies having 5 (Harmelin, 1970). The name *P. scripta* has been placed in synonymy with *P. radiata* by several authors, although it has been applied at least once to Recent material (Manzoni, 1871). It is interesting to note that the co-occurrence of the apparently closely related entities *P. venusta* and *P. scripta*/*P. radiata* in the Paratethys during Middle Miocene times persists to the present day in the Mediterranean. The taxonomic status of these forms requires clarification.

In the English Channel material studied in the present paper, *P. venusta* occurred off Brittany at depths of 82–102 m. It was reported at greater depths (180–182 m and 250–270 m) in the northern Bay of Biscay by Hayward & Ryland (1978). *P. venusta* appears to have a wide present-day latitudinal range. The most northerly material available is from deep water (320 m) off the Shetlands (BMNH 1911.10.1.732). The species was described originally from material collected off Rabat (Morocco), and has been recorded from the Canaries by Aristegui (1983; 1984) and off the eastern coast of South Africa at a depth of 90 m by Hayward & Cook (1983).

Puellina (Cribrilaria) innominata (Couch, 1844)

(Figs 50–58 and Table 8)

Lepralia innominata Couch, 1844; 114, 115, pl. 22 fig. 4.
Lepralia innominata: Johnston, 1847; 319, 320, pl. 55 fig. 12.
not *Lepralia innominata*: Busk, 1859; 40, pl. 4 fig. 2.
part or whole *Cribrilina radiata*, *innominata* form: Hincks, 1880; 185–190, pl. 25 figs 1, 2, 5.
Cribrilaria innominata: Hayward & Ryland, 1979; 64, fig. 17A–D.
Cribrilaria innominata: Bishop, 1986; 96, 98, figs 1–8.

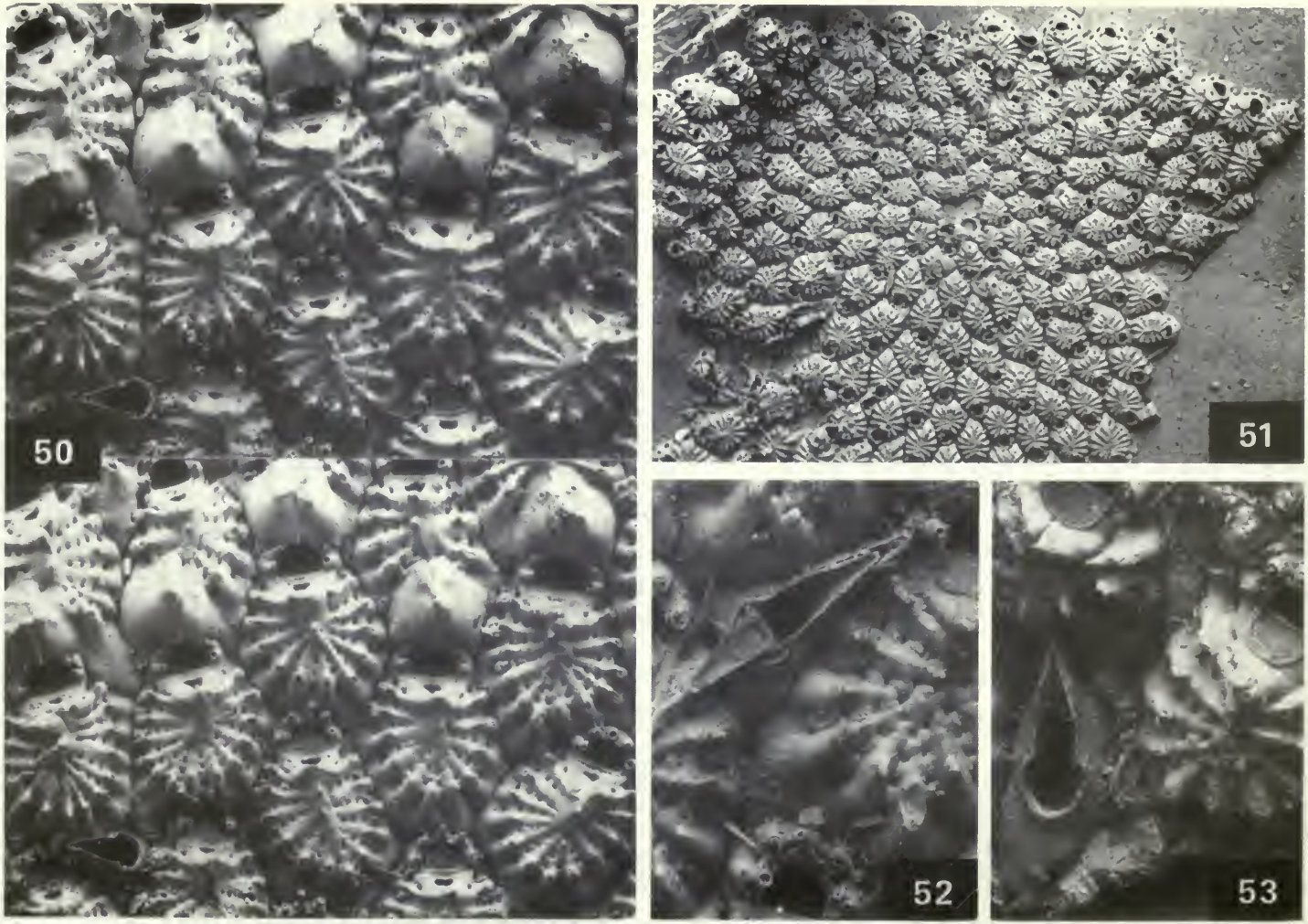
Material examined by SEM.

Neotype: 1847.9.16.32 (Goran [Cornwall]; selected by Bishop, 1986).

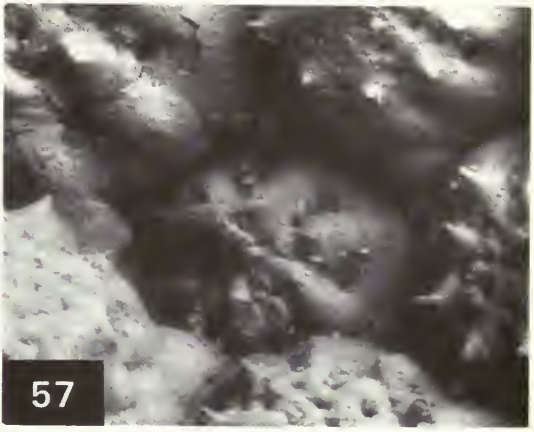
BMNH: 1897.5.1.632 (Hastings); 1899.5.1.720A (British); 1899.5.1.723 (Antrim); 1911.10.1.723 (British); 1936.12.30.335B (Liverpool Bay); 1985.11.20.41b (off Craggan Rocks, S. Cornwall); 1985.11.20.73a and 1985.11.20.76a (Channel Stn 253); 1985.11.20.102a (Channel Stn 260); 1985.11.20.103d (Channel Stn 261); 1985.11.20.116b (Channel Stn 318).

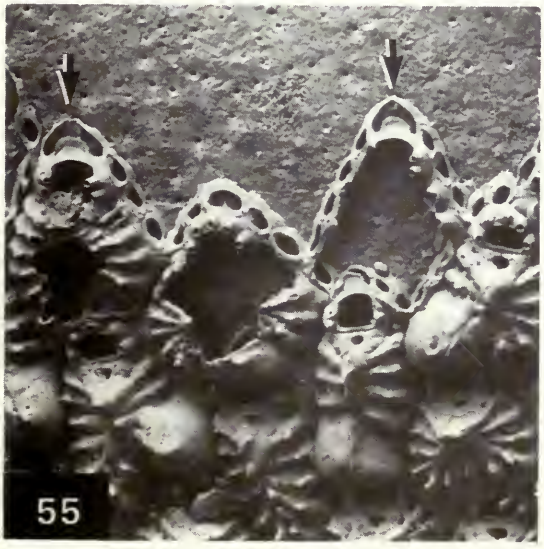
Other material.

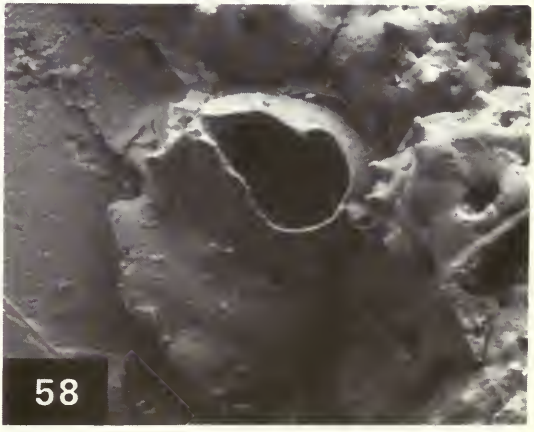
BMNH: 1847.9.16.53 (British); 1847.9.16.122 (Sana Island [W. Scotland]); 1847.9.16.161 (British, colony numbered 2); 1847.9.16.162 and 1899.5.1.720B, D (British); 1899.5.1.722 (Guernsey, colonies on three shells); 1911.10.1.720 and 1911.10.1.721 (British, numerous colonies on shell fragments); 1911.10.1.722 (Shetland, several colonies on pebbles); 1911.10.1.725 (Guernsey, several colonies on shell fragments); 1911.10.1.726 (Birturbuy [= Bertraghboy] Bay [Galway], numerous colonies on shell fragments); 1919.6.24.35 (Birterbuy [= Bertraghboy] Bay [Galway]); 1936.12.30.332A–D (Liverpool Bay); 1936.12.30.333A–J and 1936.12.30.334 (no locality [probably Liverpool Bay]); 1936.12.30.335C (Liverpool Bay); 1963.3.30.142 (Plymouth, several colonies); 1985.11.20.42a-c, 1985.11.20.43 and 1985.11.20.44a-i (off Craggan Rocks, S. Cornwall); 1985.11.20.67a (Channel Stn 251); 1985.11.20.69d, 1985.11.20.70a and 1985.11.20.72e,f (Channel Stn 252); 1985.11.20.74d and 1985.11.20.81a (Channel Stn 253); 1985.11.20.83c (Channel Stn 256); 1985.11.20.88a,b (Channel Stn 257); 1985.11.20.91b and 1985.11.20.98b (Channel Stn 258); 1985.11.20.102b (Channel Stn 260); 1985.11.20.103e (Channel Stn 261); 1985.11.20.104e-h (Channel Stn 263); 1985.11.20.105d and 1985.11.20.107c (Channel Stn 275); 1985.11.20.111a and 1985.11.20.112a (Channel Stn 315); 1985.11.20.116c-k (Channel Stn 318).



Figs 50–53 *Puellina innominata* (Couch): (50) stereo pair of BMNH 1899.5.1.720A, British, × 69; (51) part of colony, BMNH 1911.10.1.723, British, × 16; (52) avicularium, BMNH 1897.5.1.632, Hastings, × 142; (53) avicularium, same colony, × 131.







Figs 54–58 *Puellina innominata* (Couch): (54) non-ovicellate autozooid, BMNH 1899.5.1.720A, British, × 143; (55) edge of colony with abraded autozooids, arrows indicate maternal autozooids, same specimen, × 58; (56) ancestrula (partially obscured), BMNH 1985.11.20.102a, Channel Stn 260, × 164; (57) ancestrula regenerated as kenozooid (note bifid top of median proximal spine of ancestrula), BMNH 1985.11.20.116b, Channel Stn 318, × 280; (58) ancestrula regenerated as avicularium, BMNH 1985.11.20.73a, Channel Stn 253, × 200.

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material multiserial, with well over 1000 autozooids. Autozooid of variable shape in frontal view, generally sub-oval (longer than broad) but occasionally broadly bifid proximally when passing to both sides of proximal zooid. Exposed lateral gymnocyst of autozooid narrow or absent (except at edge of colony); proximal gymnocyst narrow or of moderate width, frequently with proximal extension(s) between neighbouring zooids.

Frontal shield (= pericyst) moderately to heavily calcified, with 9–14 costae (most commonly 11 or 12; sometimes more than 14 in proximally bifid zooids in which pattern of costae is partially duplicated), with prominent distal median umbo and variable median ridge proximal to umbo. Each costa with short, broad, steeply ascending basal portion (sometimes seen to bear minute pelmatidium) leading to tapering, nearly horizontal subsequent portion contributing to slightly

Table 8 *Puellina innominata* (Couch): measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	47–55	50·1	4·87	11	Lf	216–294	254	7·67	13
b		57–63	58·9	3·08	12		238–291	268	6·09	17
c		—	—	—	0		219–284	247	8·32	12
d		55–60	57·0	3·41	11		284–369	323	8·77	11
e		56	—	—	1		293–338	308	7·01	4
f		51–62	56·5	6·01	10		250–308	278	6·33	11
a	lo	79–89	83·7	3·78	11	Lfg	293–439	363	12·8	13
b		81–89	85·3	2·72	12		325–454	369	10·7	13
c		74–92	81·8	6·17	11		311–448	363	13·2	11
d		88–103	96·0	4·58	10		404–508	455	8·53	10
e		88–95	92·3	4·44	3		384–449	406	10·0	3
f		81–90	86·3	3·27	10		325–433	384	10·7	9
a	loo	89–94	91·0	3·15	3	lf	188–266	223	8·85	13
b		91–100	97·1	4·69	8		203–265	229	7·35	18
c		74–86	80·0	11·9	2		184–272	220	13·0	15
d		96–112	105	7·00	4		231–300	266	8·26	15
e		95–115	101	10·3	4		221–268	234	6·86	8
f		91–97	94·0	3·46	3		216–298	251	10·5	11
a	Lov	172–177	175	2·28	2	Lr	174–178	176	1·81	2
b		170–188	181	3·12	8		164	—	—	1
c		145–174	162	10·2	3		—	—	—	0
d		191–238	208	9·28	6		230–234	232	1·37	2
e		163–233	195	17·6	4		—	—	—	0
f		181–195	188	3·23	4		—	—	—	0
a	lov	213	—	—	1	Lav	260–267	264	2·12	2
b		195–206	200	2·00	7		180	—	—	1
c		184–229	203	12·5	3		—	—	—	0
d		192–254	229	10·4	6		318–326	322	1·98	2
e		166–214	192	13·7	3		—	—	—	0
f		201–231	215	6·29	4		—	—	—	0

a = neotype (BMNH 1847.9.16.32); b = BMNH 1899.5.1.720A; c = BMNH 1899.5.1.723; d = BMNH 1911.10.1.723; e = BMNH 1985.11.20.103d; f = BMNH 1985.11.20.76a.

convex central region of shield; tubercle or short ridge at junction of the two portions of each costa, near periphery of shield. Intercostal pores of variable shape (round, sub-oval, reniform or sub-rectangular), of relatively uniform size throughout shield, sometimes with denticles adjacent to intercostal suture; 1–5 (most commonly 3 or 4) pores between successive costae. Lipped papilla pore between bases of successive costae, considerably larger than adjacent intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, very clearly broader than long, proximal edge straight. Orifice of ovicellate zooid frequently appearing distally truncate to variable extent in frontal view because of overhanging calcification of ovicell; width 1·0–1·1 times that of orifice of non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 4 in ovicellate zooid; jointed just above base; with inwardly directed, inconspicuous half-circle of denticles near base. Apertural bar forming triangular area, sloping upwards from proximal margin of orifice to umbo; with minute pelmatidium each side of indistinct median suture; without tubercles. Single, very large median sub-oral lacuna (much larger than an intercostal pore), variable in shape but frequently sub-triangular, with base of triangle towards orifice; without denticles.

Each autozooid with 7–9 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony: Fig. 55) relatively large (as large as or larger than sub-oral lacuna).

Ovicell of category A (p. 4), length generally 0·6–0·7 times that of frontal shield of autozooid; frontal surface non-punctate, with up to 4 indistinct tubercles or short ridges in more or less radiating pattern, occasionally approximating to central umbo; frequently with median suture.

Avicularium (Figs 52, 53) infrequent to fairly frequent, interzooidal, considerably smaller than autozooid. Palate elongate-triangular, inclined at moderate angle to substrate (highest distally); rostrum generally directed between autozooids. Mandible equal in length to palate and of same shape, fitting into it. Length of proximal gymnocyst of avicularium clearly shorter than that of palate plus frontal non-calcified area. Frontal non-calcified area sometimes occupied by cribrimorph frontal shield after regeneration as kenozooid.

Kenozooid infrequent (BMNH 1985.11.20.103d only), slightly smaller than autozooid, with cribrimorph frontal shield of costae in radiating pattern; gymnocyst narrow.

Ancestrula (Fig. 56) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Details of jointing (if any) of spines not seen. Median proximal spine with strongly bifid tip (Fig. 57). Most distal pair of spines each with short, minutely denticulate, inwardly directed apophysis near base. Remaining eight erect spines each with inwardly directed spiniform apophysis (sometimes with lateral denticles and minutely bifid tip) near base. Ancestrula sometimes regenerated as kenozooid (Fig. 57), or rarely as avicularium (BMNH 1985.11.20.73a: Fig. 58).

REMARKS. The identity of *Puellina innominata* has been discussed, and a neotype selected, by Bishop (1986). The species is generally well characterised around the British Isles, where variation is largely limited to the degree of development of the costal ridges and umbo. However, many other forms apparently related to *P. innominata* as defined by the neotype are known from other parts of the world, and the elucidation of the status of these would involve an immense amount of study.

Material from the British Isles and adjacent waters studied in the present paper was collected from the English Channel off Sussex, Normandy, Brittany, Guernsey, Devon and Cornwall (depths, where known, 38–106 m); from Galway; from the Irish Sea; off Antrim; off the W. coast of Scotland; and from the Shetlands.

Puellina (Cribrilaria) bifida (d'Hondt, 1970)

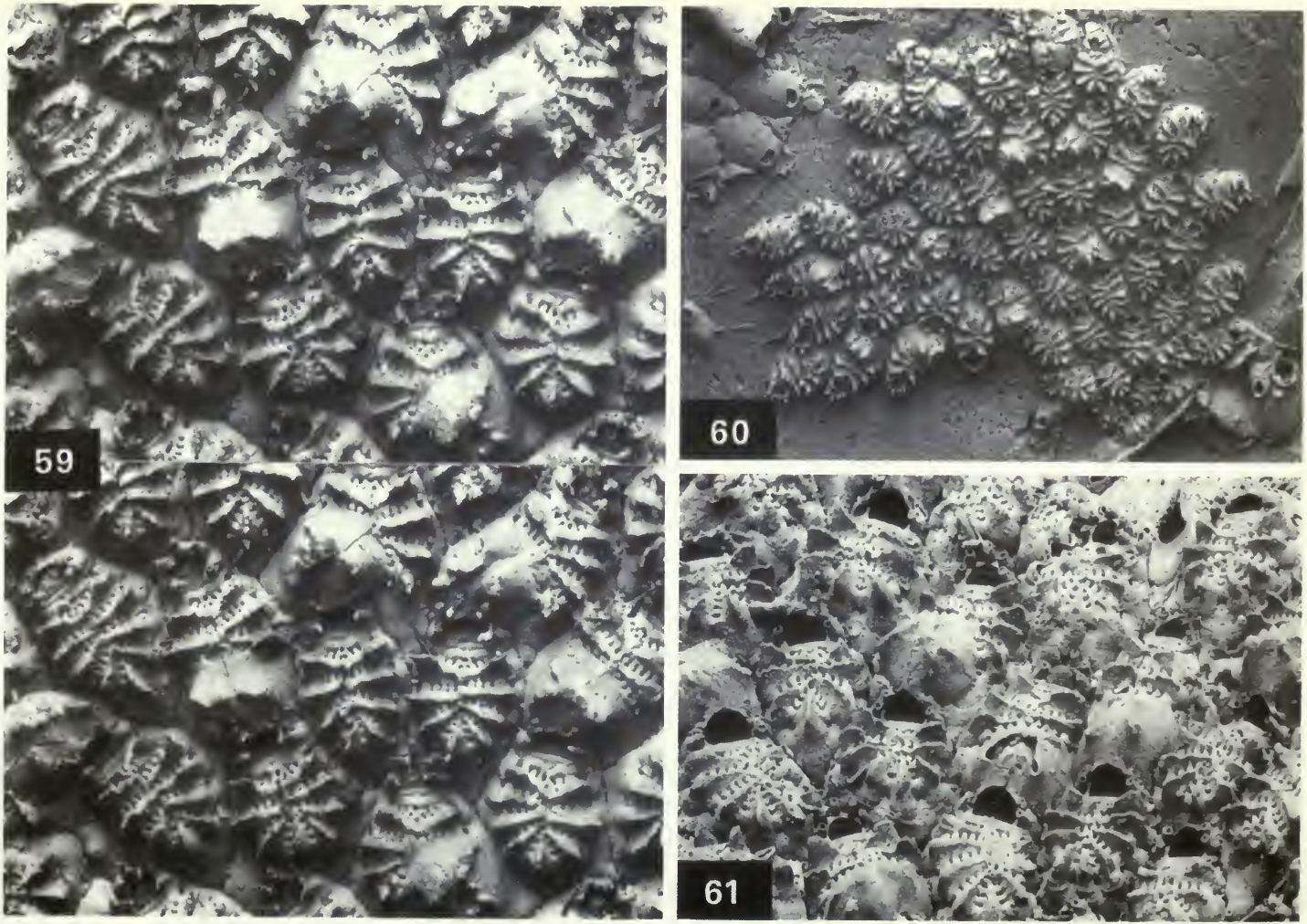
(Figs 59–72 and Table 9)

Colletosia innominata subsp. *bifida* d'Hondt, 1970; 246–248, fig. 12a-c.

MATERIAL EXAMINED BY SEM.

Lectotype (selected here); LBIMM-BRY-11603 (48°01′N, 05°44′W, 130 m).

BMNH: 1911.10.1.735B (Belfast); 1911.10.1.1182B (off Antrim); 1936.12.30.331A (two colonies) and B (no locality [probably Liverpool Bay]); 1985.11.20.41a (off Craggan Rocks, S. Cornwall); 1985.11.20.71a and 1985.11.20.72d (Channel Stn 252); 1985.11.20.94b, c (Channel Stn 258); 1985.11.20.103a (Channel Stn 261).



Figs 59–61 *Puellina bifida* (d'Hondt): (59) stereo pair of lectotype (LBIMM–BRY–11063), off Finistère, × 83; (60) whole colony, lectotype, × 30; (61) part of colony viewed at angle, BMNH 1936.12.30.331B, no locality, × *c.* 70.

OTHER MATERIAL.

BMNH: 1847.9.16.161 (British, colony numbered 1); 1899.5.1.720C (British); 1899.5.1.953 (Antrim); 1911.10.1.731 (British); 1911.10.1.737B (Guernsey); 1936.12.30.331C,D (no locality [probably Liverpool Bay]); 1936.12.30.332B and 1936.12.30.335C (Liverpool Bay); 1985.11.20.45 (Channel Stn 183); 1985.11.20.47 (Channel Stn 240); 1985.11.20.52b-d, 1985.11.20.53 and 1985.11.20.54a-e (Channel Stn 248); 1985.11.20.57a and 1985.11.20.59b-f (Channel Stn 249); 1985.11.20.60a, 1985.11.20.63a and 1985.11.20.64a-d (Channel Stn 250); 1985.11.20.69b,c (Channel Stn 252); 1985.11.20.74c and 1985.11.20.77a, b (Channel Stn 253); 1985.11.20.83a (Channel Stn 256); 1985.11.20.87a and 1985.11.20.89 (Channel Stn 257); 1985.11.20.90a,b, 1985.11.20.91a, 1985.11.20.92a, 1985.11.20.93a, 1985.11.20.94a, 1985.11.20.96a, 1985.11.20.97a and 1985.11.20.98a (Channel Stn 258); 1985.11.20.104a,b (Channel Stn 263); 1985.11.20.105a-c and 1985.11.20.107a,b (Channel Stn 275); 1985.11.20.108b-d and 1985.11.20.109b (Channel Stn 314); 1985.11.20.111b (Channel Stn 315); 1985.11.20.114 (Channel Stn 317); 1985.11.20.116a (Channel Stn 318).

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material pluriserial to multiserial, with over 200 autozooids. Autozooid of variable shape in frontal view, generally sub-oval (longer than broad). Lateral and proximal gymnocyst of autozooid narrow or of moderate width, but frequently with proximal and proximo-lateral extensions between neighbouring zooids.

Frontal shield (=pericyst) of autozooid moderately calcified, with little or no differential median thickening and no umbo, with 6–11 costae (usually 7–9). Each costa with short, broad, steeply ascending basal portion at periphery of frontal shield leading to tapering, nearly horizontal subsequent portion contributing to almost flat central region of shield. Costal ridges prominent, raised near edge of shield but lower centrally, frequently showing abrupt decrease in height between periphery and centre of shield giving characteristic appearance (especially noticeable when viewed obliquely: Fig. 61). Intercostal pores sub-rectangular or reniform, relatively uniform in size throughout shield, often with denticles adjacent to intercostal suture; usually 4, occasionally 5, pores between successive costae, but frequently fewer between short proximal costae. Lipped papilla pore between bases of successive costae, about size of adjacent intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, clearly broader than long, proximal edge straight. Orifice of ovicellate zooid frequently appearing distally truncate to varying extent in frontal view because of overhanging calcification of ovicell; width 1·1–1·2 times that of orifice of non-ovicellate zooid. Oral spines 5 in non-ovicellate zooid, 4 in ovicellate zooid; jointed at base and generally with inwardly directed spiniform apophysis near base. Apertural bar with low tubercle each side of median suture and pelmatidium on each tubercle. (Pelmatidia not observed elsewhere on shield.) Single median sub-oral lacuna between tubercles of apertural bar and first row of intercostal pores, about same size as an intercostal pore, frequently with pair of denticles on proximal margin; lacuna occasionally confluent with adjacent intercostal pores.

Each autozooid with 5–8 distolateral pore chambers; uncalcified external windows of pore chambers, seen in zooids on edge of colony (Fig. 67), relatively large (considerably larger than an intercostal pore).

Ovicell of category A or occasionally B (p. 4) (Fig. 70), length 0·7–0·9 times that of frontal shield of autozooid; frontal surface non-punctate, frequently with up to 4 ridges in more or less radiating pattern, with median suture.

Avicularium absent in holotype, infrequent in other material (Figs 65–67), interzooidal, smaller than an autozooid, nearly always seen on periphery of colony (exceptions occurring at sites of apparent disruption to colony growth in BMNH 1936.12.30.331A). Palate elongate-triangular, of somewhat variable length, often curving down towards substrate distally. Mandible elongate-triangular, sometimes with very acute tip produced beyond (? damaged or incomplete) palate as narrow down-curved extension (seen in dried material). Cystid of avicularium with 2 or 3 pore chamber windows; length of proximal gymnocyst about equal to that of palate plus frontal non-calcified area. Frontal non-calcified area sometimes occupied by cribrimorph frontal shield after regeneration as kenozooid (Fig. 69).

Kenozooid (Fig. 68) infrequent, generally smaller than an autozooid, with cribrimorph frontal shield of costae in radiating pattern.

Ancestrula (Fig. 71) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Erect spines jointed at base and with at least 2 subsequent segments. Median proximal spine with broad, sometimes slightly bifid tip. Most distal pair of spines each with short, blunt, inwardly directed apophysis near base. Remaining eight erect spines each with long, slender, inwardly directed spiniform apophysis (sometimes with minutely bifid tip) near base. Ancestrula sometimes regenerated as kenozooid (Fig. 72).

Table 9 *Puellina bifida* (d'Hondt): measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	43–49	45·7	4·21	9	Lf	198–246	222	7·02	12
b		39–53	47·3	7·85	10		199–252	216	7·40	9
c		52	—	—	1		204–208	206	1·54	2
d		52–59	54·7	3·89	14		187–295	233	12·0	14
e		—	—	—	0		195–271	227	9·02	16
a	lo	54–62	58·2	4·97	9	Lfg	251–332	287	9·17	12
b		59–73	65·3	7·16	8		243–318	276	10·9	8
c		71	—	—	1		252–253	253	0·314	2
d		61–73	65·9	6·15	14		227–426	327	19·1	14
e		—	—	—	0		262–407	310	15·8	15
a	loo	65–72	68·9	4·11	7	lf	149–179	162	6·30	15
b		79–81	80·0	1·99	2		142–191	173	8·26	11
c		75–78	76·5	3·12	2		169–187	178	8·04	2
d		68–79	74·0	4·96	6		158–221	188	10·7	18
e		—	—	—	0		157–200	175	7·39	14
a	Lov	148–184	167	9·28	6	Lr	—	—	—	0
b		155–173	162	5·33	4		144–148	146	2·18	2
c		—	—	—	0		136	—	—	1
d		146–198	175	12·7	5		142	—	—	1
e		154–177	164	6·15	5		—	—	—	0
a	lov	178–205	195	6·06	6	Lav	—	—	—	0
b		168–218	188	12·7	4		228–233	231	1·72	2
c		—	—	—	0		229	—	—	1
d		170–206	188	7·53	5		240	—	—	1
e		184–212	197	5·64	5		—	—	—	0

a = lectotype (LBIMM-BRY-11603); b = BMNH 1985.11.20.103a; c = BMNH 1936.12.30.331B; d = BMNH 1936.12.30.331A; e = BMNH 1911.10.1.1182B.

Figs 62–66 *Puellina bifida* (d'Hondt): (62) ovicellate autozooid, lectotype (LBIMM–BRY–11603), off Finistère, × 170; (63) non-ovicellate autozooid, BMNH 1985.11.20.71a, Channel Stn 252, × 240; (64) abraded autozooids at edge of colony showing pore chambers, arrows indicate intact maternal autozooids (that had presumably been ovicellate), BMNH 1936.12.30.331A, no locality, × 91; (65) avicularium, BMNH 1985.11.20.103a, Channel Stn 261, × 260; (66) avicularium, regenerated non-ovicellate autozooid (on left) with abnormal orifice and maternal autozooid (on right) with ovicell not yet developed, BMNH 1936.12.30.331B, no locality, × 150.

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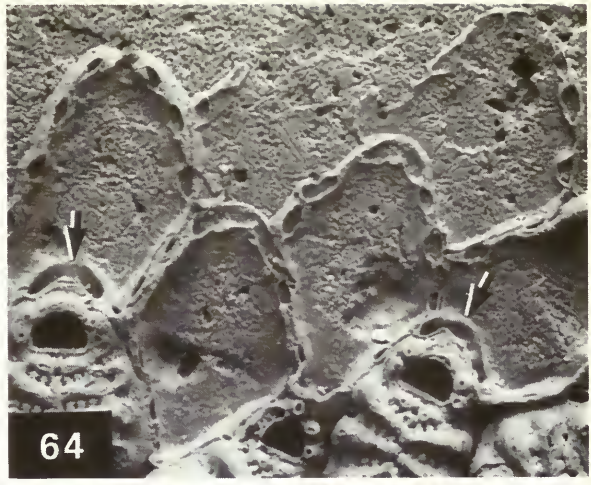
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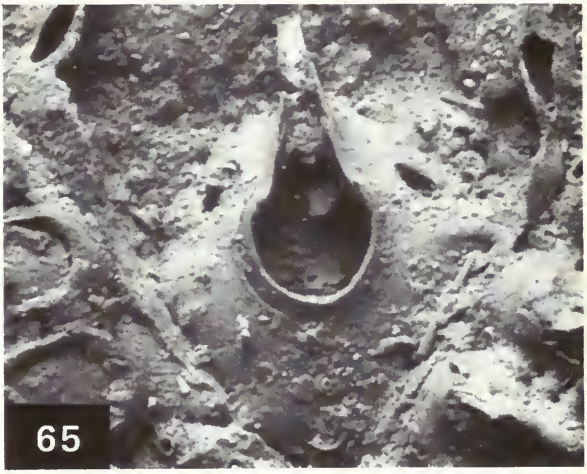
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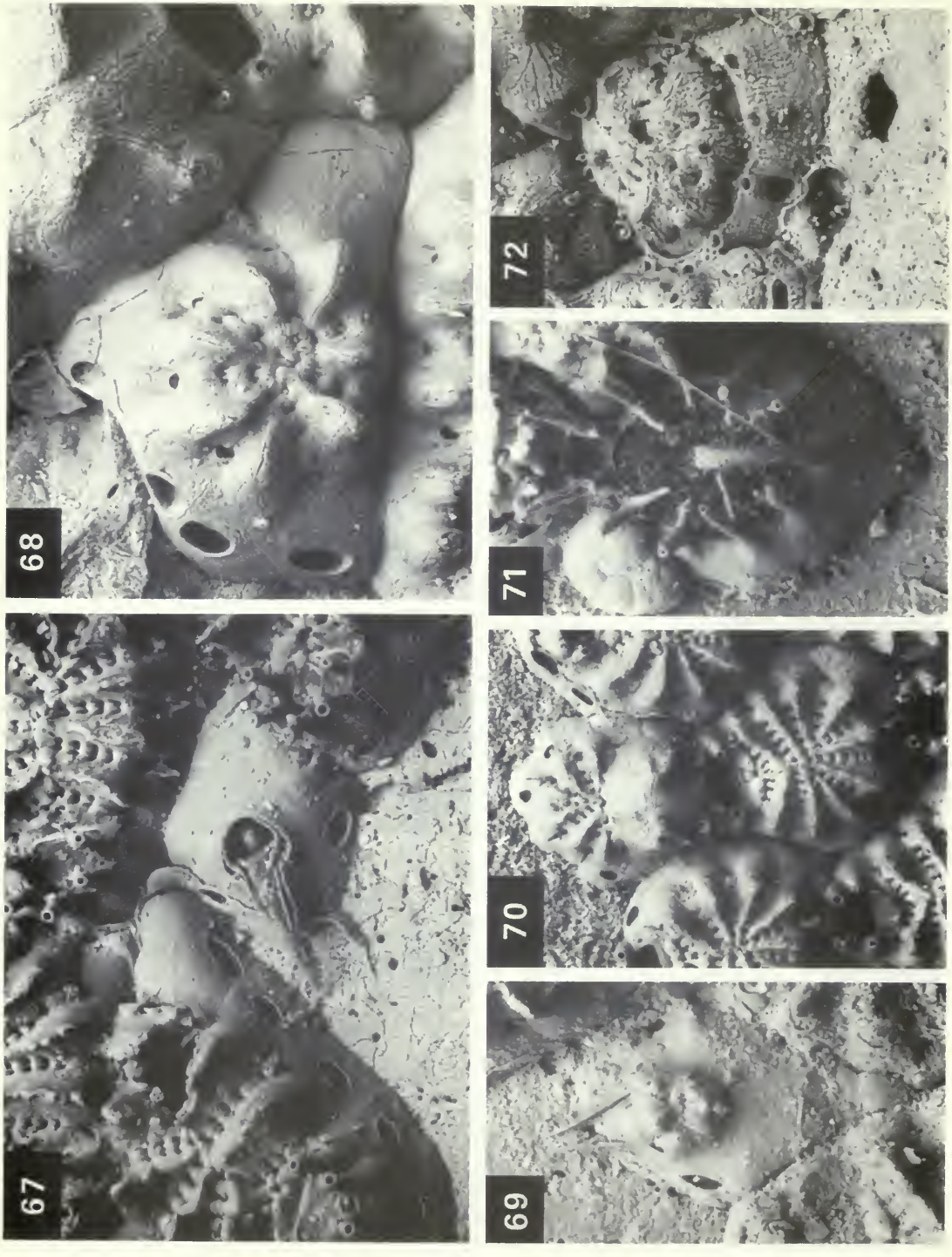
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REMARKS. This form has apparently been overlooked since its description as a subspecies of *P. innominata*. The latitude of the type locality given by d'Hondt (1970:233) is erroneous, and he provided (pers. comm. to JDDB, 1986) the correct position off Finistère quoted here. The type series comprised 'quelques colonies' but no holotype designation for these was published. The specimen received on loan from LBIMM, which was labelled 'holotype', is designated here as lectotype. It is not known whether this is the specimen figured by d'Hondt. The original account and figure clearly refer to the form represented by the lectotype, but are misleading in a number of respects. The supposedly bifid oral spines described by d'Hondt are in fact incomplete, broken just above the level of their inwardly directed apophyses. A minute apical avicularium on the ovicell, mentioned by d'Hondt in both the description and diagnosis and apparently shown in his figure 12a, is not to be seen in the lectotype, nor in other material examined here. The frontal shields of adjacent zooids are not separated by broad, smooth areas as apparently shown in figure 12a. Non-ovicellate zooids with 4, rather than 5, oral spines have not been observed.

P. bifida is extremely similar to the Badenian (Middle Miocene) fossil *P. kollmanni* (David & Pouyet, 1974) from the Vienna Basin (material of *P. kollmanni* examined by SEM: holotype and paratype, both NMV 1848/38/76; BMNH D44968 and D55589; all from Eisenstadt). The only appreciable difference between the two forms is that the avicularian palate of *P. kollmanni* is generally more elongate and slender than that of *P. bifida*, and often almost parallel sided. As mentioned above, the length of the palate in *P. bifida* is variable, and in some examples the mandible appears to pass beyond the palate as a narrow extension (Fig. 67). If it could be shown that in the latter cases the rostrum was broken short distally, the shape of the palate when complete would be inferred from the mandible to resemble that seen in *P. kollmanni*, and an argument might then be made for treating the fossil and Recent forms as conspecific.

Puellina bifida is also similar to the Recent Mediterranean species *P. minima* (Harmelin, 1984) of which four colonies of the type series (LBIMM, no registration number, Cassis, France) were examined by SEM. In *P. minima*, however, the ovicellate zooid has 2 oral spines, not 4. As noted by Harmelin (1984), the ovicell of *P. minima* may rest on a kenozooid (Fig. 94; ovicell category B of the present paper). This condition is also sometimes seen in *P. bifida* (Fig. 70). The material from the Canaries recorded as *C. minima* by Aristegui (1984) has 4 oral spines in the ovicellate zooid, and seems to be closer to *P. bifida* than to Harmelin's species.

P. bifida is known to occur off Finistère (depth 130 m); in the English Channel off Boulogne, Normandy, Brittany, Guernsey and Cornwall (at depths, where known, of 29–102 m); in the Irish Sea; and off Antrim. The presence in the Canaries of a very similar, possibly conspecific, form recorded by Aristegui (1984) as *Cribrilaria minima* suggests that *P. bifida* may also be found considerably further south than the above-mentioned localities.

***Puellina (Cribrilaria) arrecta* n.sp.**
(Figs 73–81 and Table 10)

whole or part *Cribrilaria flabellifera*: Harmelin, 1970; 94–96.
part *Cribrilaria flabellifera*: Harmelin, 1978; 186, 187 (material from Stn 72); pl. 2 figs 8, 9, 12.
Cribrilaria flabellifera: Hayward & Ryland, 1978; 146.

Holotype: BMNH 1985.11.20.108h (Channel Stn 314, 49°12·4′N 03°14·8′W, 73 m).
Paratypes (examined by SEM): BMNH: 1911.10.1.737A (Guernsey); 1985.11.20.76e–g (Channel Stn 253); 1985.11.20.82b (Channel Stn 256); 1985.11.20.103f (Channel Stn 261); 1985.11.20.110c (Channel Stn 314).

Figs 67–72 *Puellina bifida* (d'Hondt): (67) avicularium with mandible intact, BMNH 1985.11.20.71a, Channel Stn 252, ×166; (68) kenozooid, BMNH 1936.12.30.331A, no locality, ×260; (69) avicularium regenerated as kenozooid, BMNH 1985.11.20.103a, Channel Stn 261, ×200; (70) autozooid with category B ovicell, BMNH 1936.12.30.331A, no locality, ×102; (71) ancestrula, BMNH 1985.11.20.72d, Channel Stn 252, ×230; (72) ancestrula regenerated as kenozooid, BMNH 1936.12.30.331B, no locality, ×250.

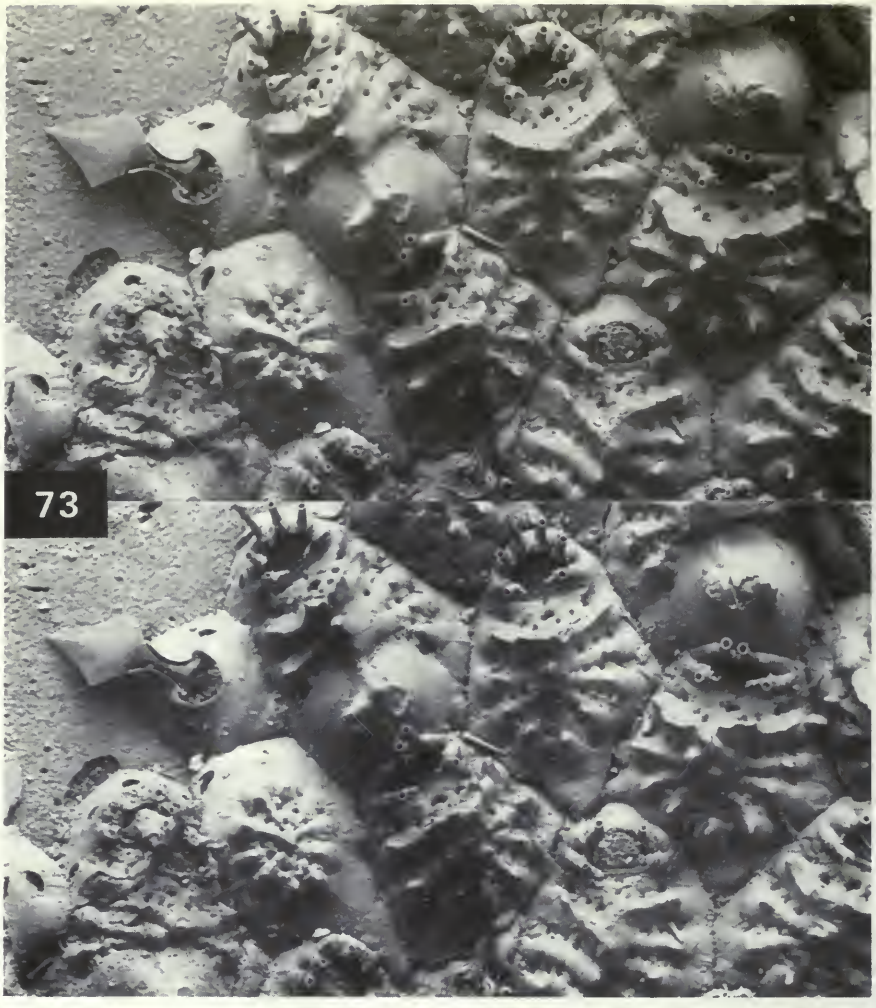

Fig. 73 *Puellina arrecta* n.sp.: stereo pair of holotype (BMNH 1985.11.20.108h), Channel Stn 314, × 111.

OTHER MATERIAL.

BMNH: 1985.11.20.35 (northern Bay of Biscay); 1985.11.20.49 and 1985.11.20.50a (Channel Stn 247); 1985.11.20.57b (Channel Stn 249); 1985.11.20.63b and 1985.11.20.64h (Channel Stn 250); 1985.11.20.69g,h and 1985.11.20.72k (Channel Stn 252); 1985.11.20.73b, 1985.11.20.75, 1985.11.20.79 and 1985.11.20.81b,c (Channel Stn 253); 1985.11.20.84 (Channel Stn 256); 1985.11.20.85a and 1985.11.20.86 (Channel Stn 257); 1985.11.20.102c (Channel Stn 260); 1985.11.20.108i,j (Channel Stn 314).

J. G. Harmelin, personal collection: three colonies from Cassidaigne (Marseille), 350–450 m.

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material pluriserial to multiserial, with over 100 autozooids. Autozooid of variable shape in frontal

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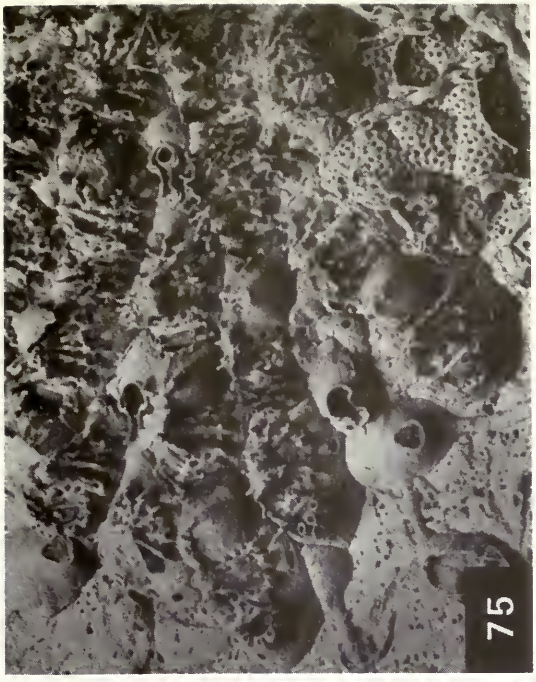
Figs 74–77 *Puellina arrecta* n.sp.: (74) whole colony, BMNH 1985.11.20.110c, Channel Stn 314, × 20; (75) edge of colony viewed at angle, BMNH 1985.11.20.76e, Channel Stn 253, × *c.* 65; (76) avicularium (mandible intact) and distal part of non-ovicellate autozooid, holotype (BMNH 1985.11.20.108h), Channel Stn 314, × 250; (77) avicularium, ovicellate and non-ovicellate autozooids, BMNH 1985.11.20.76e, Channel Stn 253, × 157.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view, generally sub-oval (longer than broad). Lateral and proximal gymnocyst of autozooid narrow or of moderate width, but frequently with proximal or proximo-lateral extensions between neighbouring zooids.

Frontal shield (=pericyst) of autozooid heavily calcified (especially near midline), with 8 or 9 costae (rarely 7 or 10). Each costa with short, steeply ascending basal portion at periphery of frontal shield leading to less steep subsequent portion contributing to convex central region of shield. Costal ridges prominent, each with tubercle (sometimes with minute pelmatidium) towards periphery of shield; ridges frequently fused to form strongly raised median ridge or umbo, especially towards distal end of shield. Intercostal pores sub-rectangular or reniform, relatively uniform in size throughout shield, often with denticles adjacent to intercostal suture; usually 2 or 3 pores between successive costae. Lipped papilla pore between bases of successive costae, slightly larger than adjacent intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, very clearly broader than long, proximal edge straight. Orifice of ovicellate zooid sometimes appearing distally truncate to varying extent in frontal view because of overhanging calcification of ovicell; width 1·0–1·1 times that of orifice of non-ovicellate zooid. Oral spines 6 in non-ovicellate zooid, 4 in ovicellate zooid; jointed some distance above base; most proximal spine on each side generally with inwardly directed spiniform apophysis above joint; remaining spines with inwardly directed half-circle of denticles above joint. Apertural bar sloping upwards from proximal margin of orifice to first row of intercostal pores, with median suture; often with minute pelmatidium on very low tubercle each side of midline. Single median sub-oral lacuna of variable shape, larger than an intercostal pore, frequently with pair of denticles on proximal margin.

Each autozooid usually with 6–8 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony: Fig. 79) of moderate size but considerably larger than an intercostal pore.

Ovicell of category A (p. 4), length 0·6–0·9 times that of frontal shield; frontal surface non-punctate, with up to 3 low ridges in more or less radiating pattern; median suture occasionally discernible.

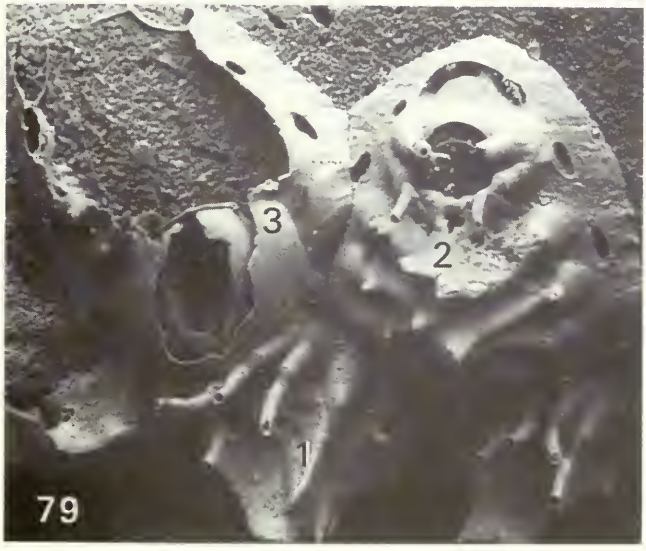
Avicularium (Fig. 76) frequent, interzooidal, total length (excluding mandible) approximately equal to that of frontal shield of autozooid. Palate flared at each end with relatively narrow middle portion; margins smooth (rarely with irregular minute crenulations). Mandible clearly longer than palate, broadening laterally beyond palate into angular-ovate or triangular blade *c.* 1·5 times as wide as frontal non-calcified area of cystid. Frontal non-calcified area sometimes occupied by cribrimorph frontal shield after regeneration as kenozooid (Fig. 78). Cystid of avicularium with 2 or 3 pore chambers. Length of proximal gymnocyst about equal to that of palate plus frontal non-calcified area.

Kenozooid (Fig. 73) fairly frequent, up to size of autozooid, with cribrimorph frontal shield of costae in radiating pattern.

Ancestrula (Fig. 80) tatiform, with median proximal spine overarching frontal surface plus 5 pairs of erect spines around edge of gymnocyst (i.e. total of 11 spines). Erect spines jointed, with at least 2 segments above base. Median proximal spine with broad or bifid tip. Most distal pair of spines each with short, inwardly directed apophysis near base. Remaining eight erect spines each with inwardly directed spiniform apophysis near base. Ancestrula sometimes regenerated as kenozooid (Fig. 81).

ETYMOLOGY. L. *arrectus*—upright, steep; referring to the form of the frontal shield in this species.

REMARKS. This species is most closely comparable to *P. flabellifera* (Kirkpatrick, 1888) with which it has been confused and which is redescribed below. The autozooids have more extensive exposed gymnocyst in *Puellina arrecta* n.sp. than in *P. flabellifera*. There are considerable differences in the form of the frontal shield between the two species. The frontal shield of *P. arrecta* is markedly convex whereas that of *P. flabellifera* is almost flat. There are fewer costae in *P. arrecta*. The costae all bear a ridge and/or tubercle in the newly described species, whereas only the most distal pair have distinct ornamentation (ridges) in *P. flabellifera*. The median umbo of *P. flabellifera* (when



Figs 78–81 *Puellina arrecta* n.sp.: (78) kenozooid and avicularium regenerated as kenozooid, BMNH 1985.11.20.110c, Channel Stn 314, × 230; (79) maternal autozooids (numbered 1 and 2) and developing autozooid (numbered 3) with incomplete category A ovicell for zooid 1, holotype (BMNH 1985.11.20.108h), Channel Stn 314, × 155; (80) ancestrula and first autozooid (developed to right of midline of ancestrula because of foreign body distal to ancestrula), BMNH 1985.11.20.76g, Channel Stn 253, × 200; (81) ancestrula regenerated as kenozooid, holotype, × 250.

Table 10 *Puellina arrecta* n.sp.: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	36–45	38·8	11·0	5	Lf	163–209	187	8·85	10
b		43–47	44·7	2·90	7		187–204	193	3·58	8
c		41	—	—	1		179–193	184	2·90	8
d		40–45	42·6	4·48	11		154–210	185	7·72	18
a	lo	57–65	61·0	5·30	5	Lfg	203–291	253	14·2	9
b		65–75	70·0	6·79	5		244–312	276	8·69	8
c		58	—	—	1		213–291	248	11·0	6
d		59–71	65·3	6·39	7		233–325	272	11·1	16
a	loo	63–65	64·0	2·49	2	lf	148–178	163	6·60	11
b		64–70	66·7	4·96	3		144–181	159	8·21	10
c		—	—	—	0		135–151	146	4·23	7
d		69–74	71·0	2·77	5		135–178	155	7·21	16
a	Lov	143–163	151	6·22	4	Lr	109–114	112	3·57	2
b		115–146	133	10·2	5		113–132	122	6·86	5
c		125–150	138	8·48	4		—	—	—	0
d		128–157	147	7·08	6		91–127	115	13·0	6
a	lov	155–203	181	12·5	4	Lav	208–220	214	4·47	2
b		163–193	182	6·59	5		201–262	224	11·2	5
c		170–184	177	4·31	3		—	—	—	0
d		165–180	171	4·43	6		198–296	253	16·2	5

a = holotype (BMNH 1985.11.20.108h); b = BMNH 1985.11.20.76e; c = BMNH 1911.10.1.737A; d = BMNH 1985.11.20.110c.

present) is restricted to the region of the first pair of costae, but that of *P. arrecta* generally extends proximally as a median ridge. The sub-oral lacuna is relatively smaller in *P. arrecta*, and the orifice wider but shorter. The margins of the avicularian palate are generally smooth in *P. arrecta* rather than crenulate as in *P. flabellifera*. The mandible of the avicularium is relatively small in *P. arrecta*, and broadens beyond the palate to less than twice the width of the frontal non-calcified area of the avicularian cystid, as opposed to *c.* three times the width in *P. flabellifera*.

BMNH 1985.11.20.35 is part of the material recorded as *Cribrilaria flabellifera* by Hayward & Ryland (1978). Material from the Marseille region at a depth of 350–450 m recorded as *C. flabellifera* by Harmelin (1970) was examined on loan, and is also referred to *P. arrecta* n.sp. Harmelin's material from 105–110 m in the same region was not examined.

P. arrecta is known from the English Channel off Brittany (depths 64–106 m) and Guernsey, from the northern Bay of Biscay at a depth of 180–182 m, and from the Mediterranean near Marseille (depth 350–450 m).

Puellina (Cribrilaria) flabellifera (Kirkpatrick, 1888)

(Figs 92, 93 and Table 11)

Cribrilina radiata var. *flabellifera* Kirkpatrick, 1888; 75, pl. 10 fig. 4.

Lectotype (selected here): BMNH 1888.1.25.10A (Mauritius).

DESCRIPTION OF LECTOTYPE. Fragment of unilaminar colony, zooids distinct, *c.* 90 autozooids and *c.* 50 avicularia. Autozooid of variable shape in frontal view, generally sub-oval (longer than

broad). Exposed lateral gymnocyst of autozooid narrow or absent (except at edge of colony); proximal gymnocyst narrow, but occasionally with short proximal extension(s) between neighbouring zooids.

Frontal shield (=pericyst) of autozooid moderately calcified, without differential median thickening apart from distal umbo (see below), generally with 14 or 15 costae (occasionally 16). Each costa with short, steeply ascending basal portion at periphery of frontal shield leading to nearly horizontal subsequent portion, of relatively constant width, contributing to almost flat central region of shield. Most distal pair of costae forming shallow V in frontal view, ridges prominent and frequently forming truncate median umbo. Remaining costae low, lacking distinct ornamentation. Intercostal pores sub-rectangular or reniform, relatively uniform in size throughout shield, frequently with denticles adjacent to intercostal suture; usually 4 or 5 pores between successive costae, but fewer between short proximal costae. Lipped papilla pore between bases of successive costae.

Orifice of non-ovicellate autozooid D-shaped, slightly broader than long, proximal edge straight. Orifice of ovicellate zooid generally appearing distally truncate in frontal view because of overhanging calcification of ovicell; width 1·1–1·2 times that of orifice of non-ovicellate zooid. Oral spines 6 in non-ovicellate zooid, 4 in ovicellate zooid; jointed some distance above base, apparently without apophyses (but undamaged spines not observed). Apertural bar sloping slightly upwards from proximal margin of orifice towards first pair of costae; without tubercles; sometimes with minute pelmatidium each side of median suture. (Pelmatidia not observed elsewhere on shield.) Single median sub-oral lacuna very large (considerably larger than an intercostal pore), of variable shape, frequently with denticles on lateral and proximal margins.

Characters of pore chambers not discernible.

Ovicell of category A (p. 4), length generally 0·6–0·7 times that of frontal shield of autozooid; frontal surface non-punctate, frequently with up to 4 ridges in more or less radiating pattern (or occasionally with short median ridge), with median suture.

Avicularium frequent, interzooidal, total length excluding mandible approximately equal to that of frontal shield of autozooid. Palate flared at each end, more so distally, with relatively narrow middle portion; margins crenulate. Mandible clearly longer than palate, broadening abruptly beyond palate to *c.* 3 times width of frontal non-calcified area; further details of shape not discernible because of damage. Length of proximal gymnocyst of avicularium about equal to that of palate plus frontal non-calcified area. Cystid with pore chamber windows, 3 in only example counted.

Kenozooid infrequent, smaller than an autozooid, with cribrimorph frontal shield of costae in radiating pattern.

Colony origin, including ancestrula, missing.

REMARKS. Kirkpatrick (1888: pl. 10 fig. 4) illustrated the undamaged avicularian mandible broadening rapidly beyond the palate into a sub-triangular blade. Neither Kirkpatrick's account nor the relevant BMNH accessions book indicates how many colonies were originally referred to

Table 11 *Puellina flabellifera* (Kirkpatrick): measurements on lectotype (BMNH 1888.1.25.10A) in microns

	Range	Mean	C.V.	n		Range	Mean	C.V.	n
Lo	45–53	48·6	6·32	13	Lf	184–271	213	12·6	10
lo	51–65	58·2	7·08	10	Lfg	237–340	283	12·7	11
loo	64–70	67·3	4·92	3	lf	152–208	184	8·77	15
Lov	122–167	149	12·4	5	Lr	119–156	138	11·2	15
lov	145–171	157	7·44	5	Lav	240–316	269	8·36	15

Cribrilina radiata var. *flabellifera*. Two specimens from Mauritius, stored separately but both registered as BMNH 1888.1.25.10, are the only available material referable to the original description. The specimen on a microslide, clearly the form described by Kirkpatrick and labelled 'Type', is presumably that examined by Harmelin (1978); it is here selected as lectotype (now BMNH 1888.1.25.10A). It is not possible to identify the lectotype positively as the specimen figured by Kirkpatrick. However the second, boxed, specimen (now 1888.1.25.10B) apparently grew on a different substrate from the lectotype, and is not the same species but a form with a slender elongate-triangular avicularian mandible, probably *P. africana* (Hayward & Cook, 1983).

Kirkpatrick's variety was elevated to species rank by Harmelin (1970). In addition to the original description and another record from the Indian Ocean (Thornely, 1912), the name *flabellifera* has been applied to material from the Indonesian region (Harmer, 1926; Canu & Bassler, 1929a; Winston, 1986), the central Pacific (Harmelin, 1978), the eastern Pacific (Soule, 1959), the western Caribbean (Banta & Carson, 1978; Winston, 1984), the Mediterranean (Harmelin, 1970) and the

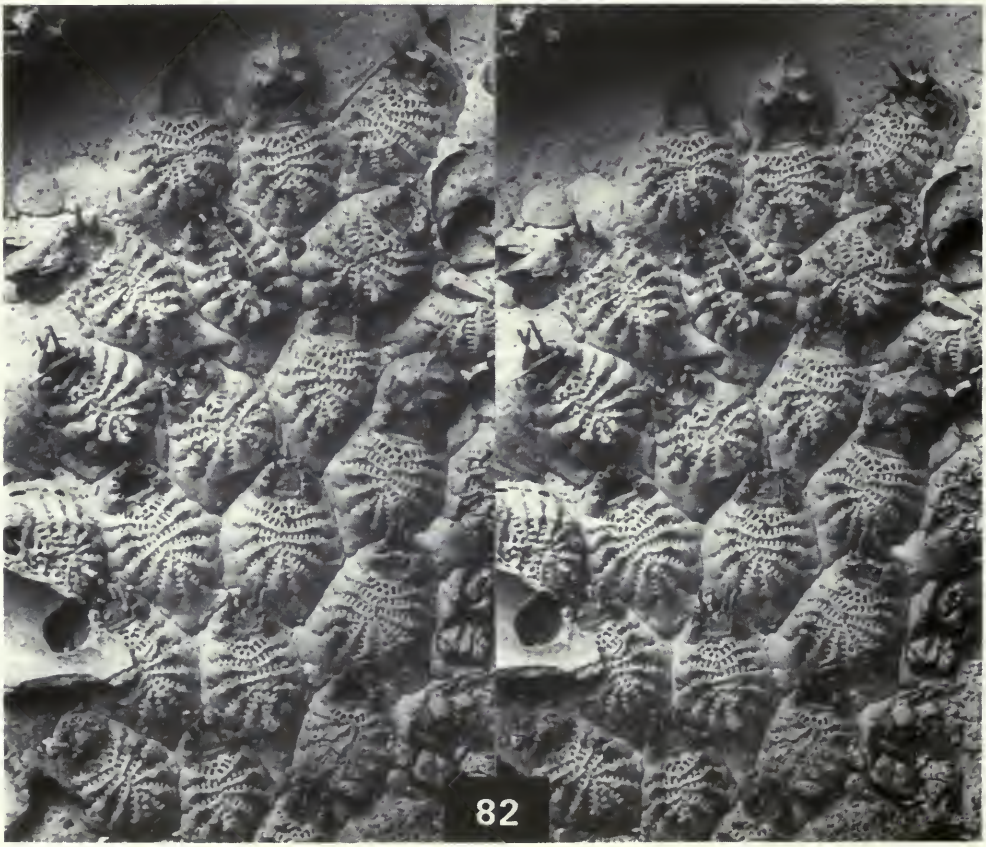


Fig. 82 *Puellina corbula* n.sp.: stereo pair of holotype (BMNH 1985.11.20.80), Channel Stn 253, × 62.

Figs 83–87 *Puellina corbula* n.sp.: (83) ovicellate and non-ovicellate autozooids at edge of colony, holotype (BMNH 1985.11.20.80), Channel Stn 253, × 133; (84) edge of colony viewed at angle, holotype, × 72; (85) avicularium recumbent on neighbouring autozooid, holotype, × 350; (86) semi-erect avicularia at edge of colony, with ovicellate and non-ovicellate autozooids, BMNH 1985.11.20.100b, Channel Stn 260, × 158; (87) kenozooid, ovicellate and non-ovicellate autozooids at edge of colony, BMNH 1911.10.1.735B, Belfast, × 112.

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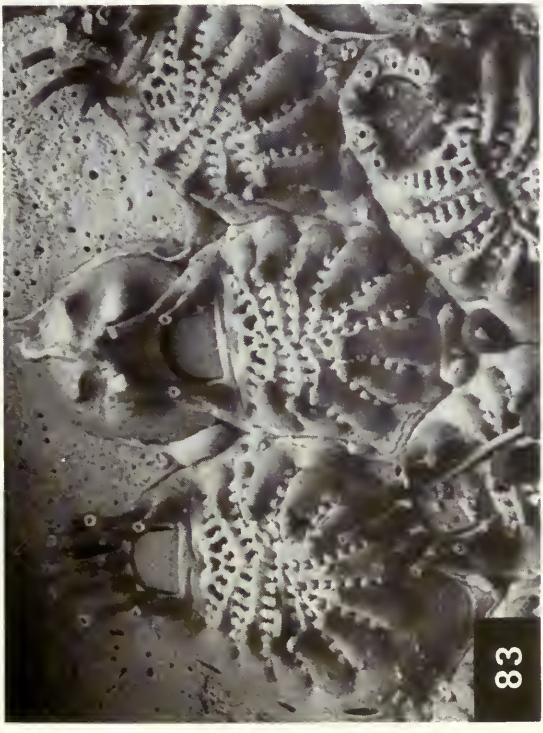
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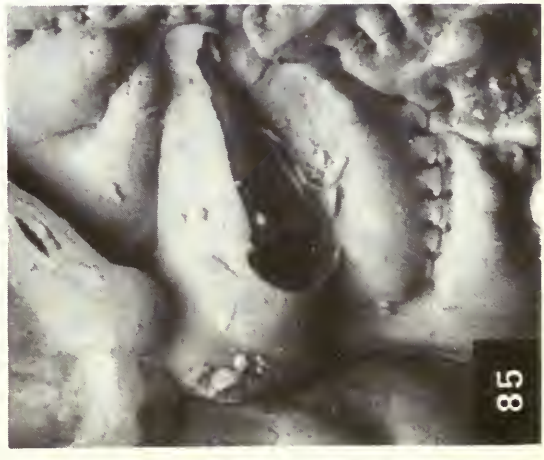
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eastern Atlantic (Harmelin, 1978; Hayward & Ryland, 1978; d'Hondt, 1979; Aristegui, 1983; 1984). It seems probable that a species group, rather than a single species, is involved. At least part of Harmelin's (1970) Mediterranean material, part of the NE. Atlantic material recorded by the same author (1978), and the record by Hayward & Ryland (1978) from the northern Bay of Biscay, are referred to *P. arrecta* n.sp. above.

Puellina (Glabrilaria) corbula n.sp.
(Figs 82–91 and Table 12)

part *Cribrilaria pedunculata*: Harmelin 1978; 188, 189 (material from Stn 72); pl. 1 fig. 5; not pl. 1 fig. 6.

Holotype: BMNH 1985.11.20.80 (Channel Stn 253, 48°52·2′N 03°54·0′W, 79 m).

Paratypes (examined by SEM): BMNH: 1911.10.1.735B (Belfast); 1985.11.20.72c (Channel Stn 252); 1985.11.20.100a,b,c (Channel Stn 260); 1985.11.20.108a and 1985.11.20.109a (Channel Stn 314).

OTHER MATERIAL.

BMNH: 1911.10.1.731 (British); 1985.11.20.52a (Channel Stn 248); 1985.11.20.59a (Channel Stn 249); 1985.11.20.69a and 1985.11.20.72a,b (Channel Stn 252); 1985.11.20.74a,b (Channel Stn 253); 1985.11.20.99 and 1985.11.20.101 (Channel Stn 260).

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colonies in available material pluriserial to multiserial, with over 200 autozooids. Autozooid of variable shape in frontal view, generally round or sub-oval (longer than broad). Lateral and proximal gymnocyst of autozooid narrow to broad, but generally of moderate width and frequently with proximal and proximolateral extensions between neighbouring zooids.

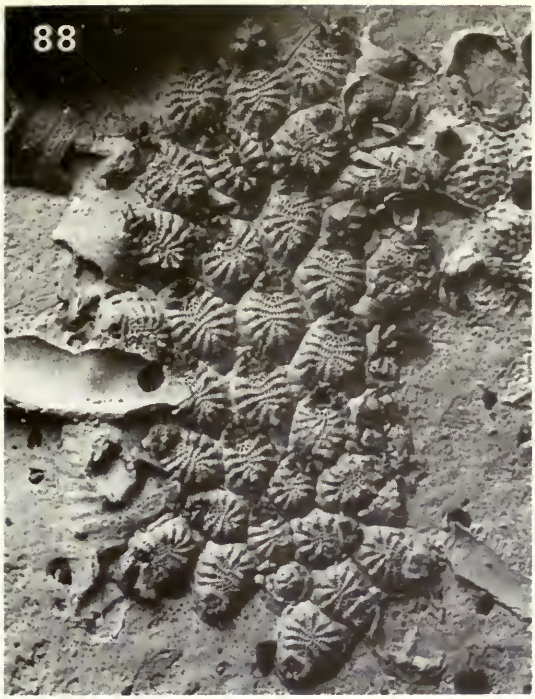
Frontal shield (=pericyst) of autozooid lightly to moderately calcified, without umbo or any other median thickening, with 9–14 costae (usually 10–12). Each costa with broad, steeply ascending basal portion at periphery of frontal shield leading to narrower, tapering, nearly horizontal subsequent portion contributing to almost flat central region of shield, and with tubercle or short ridge (frequently bearing pelmatidium) near base. Intercostal pores sub-rectangular or reniform, generally slightly larger in first intercostal row (i.e. just proximal to orifice) than in remainder of shield, frequently with denticles adjacent to intercostal suture; intercostal pores present along entire length of costae (i.e. not restricted to nearly horizontal region of shield as in many other species: Fig. 83); usually 6–8 pores between successive costae, but occasionally fewer between short proximal costae. Papilla pore between bases of successive costae inconspicuous, about size of adjacent intercostal pore.

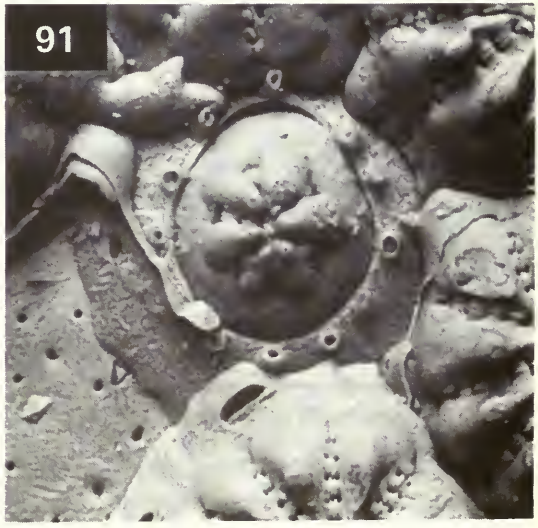
Orifice of non-ovicellate autozooid D-shaped, slightly broader than long, proximal edge straight. Orifice of ovicellate zooid occasionally appearing slightly truncate in frontal view because of overhanging calcification of ovicell; width 1·2–1·3 times that of orifice of non-ovicellate zooid. Operculum sometimes with central tubercle (Fig. 89, partially obscured). Oral spines 7 in non-ovicellate zooid, 4 in ovicellate zooid; jointed some distance above base with 2 (possibly more) subsequent segments, without inwardly directed apophyses. Distal portion of apertural bar frequently sloping downwards from proximal margin of orifice towards sub-oral lacunae; proximal portion ascending or flat; apertural bar with pelmatidium each side of midline, without tubercles. One or 2 (rarely 3) median sub-oral lacunae between proximal margin of orifice and first row of intercostal pores, of variable shape, about same size as a large intercostal pore, occasionally divided in two by median denticle.

Each autozooid with *c.* 7 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony: Fig. 84) of moderate size but considerably larger than an intercostal pore.

Ovicell of category C (p. 4), length 0·7–0·8 times that of frontal shield; frontal surface non-punctate, frequently with 4–6 low ridges in more or less radiating pattern; median suture not observed.

Avicularium (Figs 85, 86) minute, infrequent to fairly frequent; palate elongate-triangular, inclined at steep angle to substrate (except one example in holotype, with rostrum recumbent on





Figs 88–91 *Puellina corbula* n.sp.: (88) whole colony, holotype (BMNH 1985.11.20.80), Channel Stn 253, × 36; (89) non-ovicellate autozooid, holotype, × 270; (90) ancestrula and first autozooid, BMNH 1985.11.20.72c, Channel Stn 252, × 191; (91) ancestrula regenerated as kenozooid, holotype, × 230.

neighbouring autozooid: Fig. 85); rostrum curved at extreme tip to form very small beak-like projection. Mandible elongate-triangular, slightly shorter than palate. Cystid of avicularium forming short, sub-conical, semi-erect support for rostrum; with 1 or 2 pore chamber windows near base.

Kenozooid (Fig. 87) infrequent, with cribrimorph frontal shield of costae in radiating pattern.

Ancestrula (Fig. 90) tatiform, with 5 pairs of spines plus unpaired proximal and distal median spines (i.e. total of 12 spines) around edge of gymnocyst. Median proximal spine overarching frontal surface, with tapering, pointed tip; remaining spines erect, without inwardly directed (or other) apophyses. Details of jointing of spines not clearly seen, but at least some erect spines jointed at base and with at least 2 subsequent segments. Ancestrula sometimes regenerated as kenozooid (Fig. 91).

Table 12 *Puellina corbula* n.sp.: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	51–62	56·6	6·21	14	Lf	198–263	225	7·72	17
b		57–69	62·4	4·23	8		214–257	235	5·92	13
c		58–67	62·6	5·01	10		229–270	245	4·82	17
d		54–61	57·4	4·50	8		201–243	222	5·45	20
a	lo	57–68	62·7	4·69	14	Lfg	261–450	311	15·2	16
b		68–73	70·3	1·80	8		264–349	304	9·10	13
c		66–80	70·5	6·50	8		262–373	324	11·0	16
d		57–66	60·7	5·50	15		245–341	278	8·92	20
a	loo	69–78	73·5	9·74	2	lf	172–225	193	6·99	17
b		78–89	83·8	4·78	4		187–243	217	7·95	12
c		83–88	86·0	3·34	3		195–243	226	5·75	17
d		71–80	76·8	5·46	4		179–233	204	7·38	19
a	Lov	152–153	153	0·522	2	Lr	114	—	—	1
b		145–159	152	4·99	3		—	—	—	0
c		151–172	160	4·50	6		—	—	—	0
d		174–182	178	2·31	4		—	—	—	0
a	lov	186–192	189	2·53	2	Lav	149	—	—	1
b		192–199	196	1·95	3		—	—	—	0
c		182–198	194	3·32	6		—	—	—	0
d		196–222	211	5·50	4		—	—	—	0

a = holotype (BMNH 1985.11.20.80); b = 1985.11.20.100b; c = 1985.11.20.100c; d = BMNH 1911.10.1.735B.

ETYMOLOGY. L. *corbula*—a little basket; referring to the form of the frontal shield in this species.

REMARKS. *Puellina corbula* n.sp. is most closely comparable with *P. africana* (Hayward & Cook, 1983), of which two paratype colonies from the E. coast of South Africa (BMNH 1983.11.5.75) have been examined by SEM. The steeply ascending basal portion of each costa is relatively much shorter in *P. africana* than in *P. corbula* so that the frontal shield is considerably less raised overall. Unlike *P. corbula*, the costae of *P. africana* are without distinct ornamentation (the small tubercles noted in the original description not being apparent in the material examined). The avicularian rostrum is much more elongate in *P. africana*, and avicularia commonly occur closely applied to the sides of ovicells, a position they rarely occupy in *P. corbula*.

P. corbula is also similar to the Mediterranean species *P. pedunculata* Gautier, 1956, with which it has been confused (and which is redescribed below). In Gautier's species the frontal shield is more evenly convex, and the costae lack any trace of the tubercles or short ridges commonly seen near their base in *P. corbula*. Non-ovicellate autozooids of *P. corbula* have 7 oral spines, but there are only 6 in *P. pedunculata*. The avicularium of *P. corbula* has a relatively broad base (with 1 or 2 pore chamber windows) generally seen to rest on the substrate, and tapers from the base towards the rostrum, whereas that of *P. pedunculata* is fully erect and broadens slightly from a narrow base (without pore chamber windows) approximately equal in area to the uncalcified external window of the pore chamber from which it was budded. Unlike *P. pedunculata*, no area of kenozooidal costate frontal shield is seen distal to the ovicell in *P. corbula* (category C rather than category B ovicell as defined on p. 4). The ovicell of *P. corbula* is larger than that of *P. pedunculata*, both in absolute terms and relative to the respective autozooids, and generally has several ridges in a more or less radiating pattern rather than a single longitudinal ridge.

P. corbula is known from the English Channel off Brittany at depths of 73–106 m, and also from a single specimen (BMNH 1911.10.1.735B) labelled simply 'Belfast'. Specimens very similar to *P. corbula* n.sp. also occur in the Mediterranean near Marseille (J. G. Harmelin, pers. comm. to JDDB, 1986). In Harmelin's material tubercles or short ridges near the base of the costae are poorly developed or absent, and the frontal shield has a more evenly arched appearance than is usual in the material described here. However, the avicularium and ovicell are typical of *P. corbula*, and it seems probable that the Atlantic and Mediterranean forms are conspecific. This record allows the possibility that *P. corbula* is merely a geographical variant of *P. pedunculata* to be discounted, since the type locality of Gautier's species is near Marseille.

Puellina (Glabrilaria) pedunculata Gautier, 1956
(Figs 95–97 and Table 13)

Puellina pedunculata Gautier, 1956; 203, fig. 20.
Colletosia pedunculata: Prenant & Bobin, 1966; 596, 597, fig. 207III.
not *Colletosia pedunculata*: Harmelin, 1968; 1199, fig. 3(5).
Cribrilaria pedunculata: Harmelin, 1970; 93, 94, fig. 1g,h, pl. 2 fig. 6.
not *Cribrilaria pedunculata*: Harmelin, 1978; 188, 189 (material from Stn 72), pl. 1 fig. 5 (= *Puellina corbula* n.sp.).

MATERIAL EXAMINED BY SEM.
Type series: LBIMM-BRY-10384 (Marseille, two colonies on separate substrates; lectotype selected below).
BMNH: 1970.6.1.13 (Marseille).

OTHER MATERIAL.
BMNH: 1975.1.12.185 (Chios).

DESCRIPTION. Colony encrusting, unilaminar, zooids distinct; largest colony in available material with *c.* 55 autozooids. Autozooid of variable shape in frontal view, generally round or sub-oval (longer than broad). Lateral and proximal gymnocyst of autozooid narrow or of moderate width, frequently with proximal and proximo-lateral extensions between neighbouring zooids.

Frontal shield (= pericyst) lightly to moderately calcified, with little or no differential median thickening and no umbo, with 10–15 costae (usually 11–13). Each costa with short moderately to steeply ascending basal portion leading to tapering or parallel-sided nearly horizontal subsequent portion contributing to slightly convex central region of shield. Costae lacking distinct ornamentation; pelmatidia not observed. Intercostal pores sub-rectangular, relatively uniform in size throughout shield, sometimes with indistinct denticles adjacent to intercostal suture; 3–7 pores between successive costae. Lipped papilla pore between bases of successive costae, larger than adjacent intercostal pore.

Orifice of non-ovicellate autozooid D-shaped, clearly broader than long, proximal edge straight. Orifice of ovicellate zooid sometimes appearing distally truncate in frontal view because of overhanging calcification of ovicell (BMNH 1970.6.1.13); width *c.* 1·1 times that of orifice of non-ovicellate zooid. Oral spines 6 in non-ovicellate zooid, 4 in ovicellate zooid, jointed some distance

93

95

92

94

above base; further details of spine morphology not seen. Distal portion of apertural bar frequently sloping steeply downwards from proximal margin of orifice; proximal portion of apertural bar sloping slightly upwards to first pair of costae; without pelmatidia or tubercles, but median suture often discernible. Usually 2 median sub-oral lacunae, each about size of an intercostal pore, sometimes with indistinct denticles on proximal margin.

Each autozooid with *c.* 10 distolateral pore chambers; uncalcified external windows of pore chambers (seen in zooids on edge of colony) of moderate size but considerably larger than an intercostal pore.

Ovicell of category B (p. 4), with relatively small area of kenozooidal frontal shield (Fig. 95), length 0·5–0·7 times that of frontal shield of autozooid; frontal surface non-punctate, with low median ridge along entire length, frequently with central umbo.

Avicularium (Figs 95, 97) minute, frequent, often budded from kenozooid. Palate elongate-triangular, inclined at steep angle to substrate. Mandible elongate-triangular, slightly shorter than palate. Cystid erect, arising from very narrow base, an elongate, inverted cone, without pore chamber windows.

Kenozooid (Fig. 96) frequent, of variable size and shape but always smaller than autozooid, with strongly convex cribrimorph frontal shield of costae in radiating pattern. Each ovicell invariably associated with a kenozooid, as noted above.

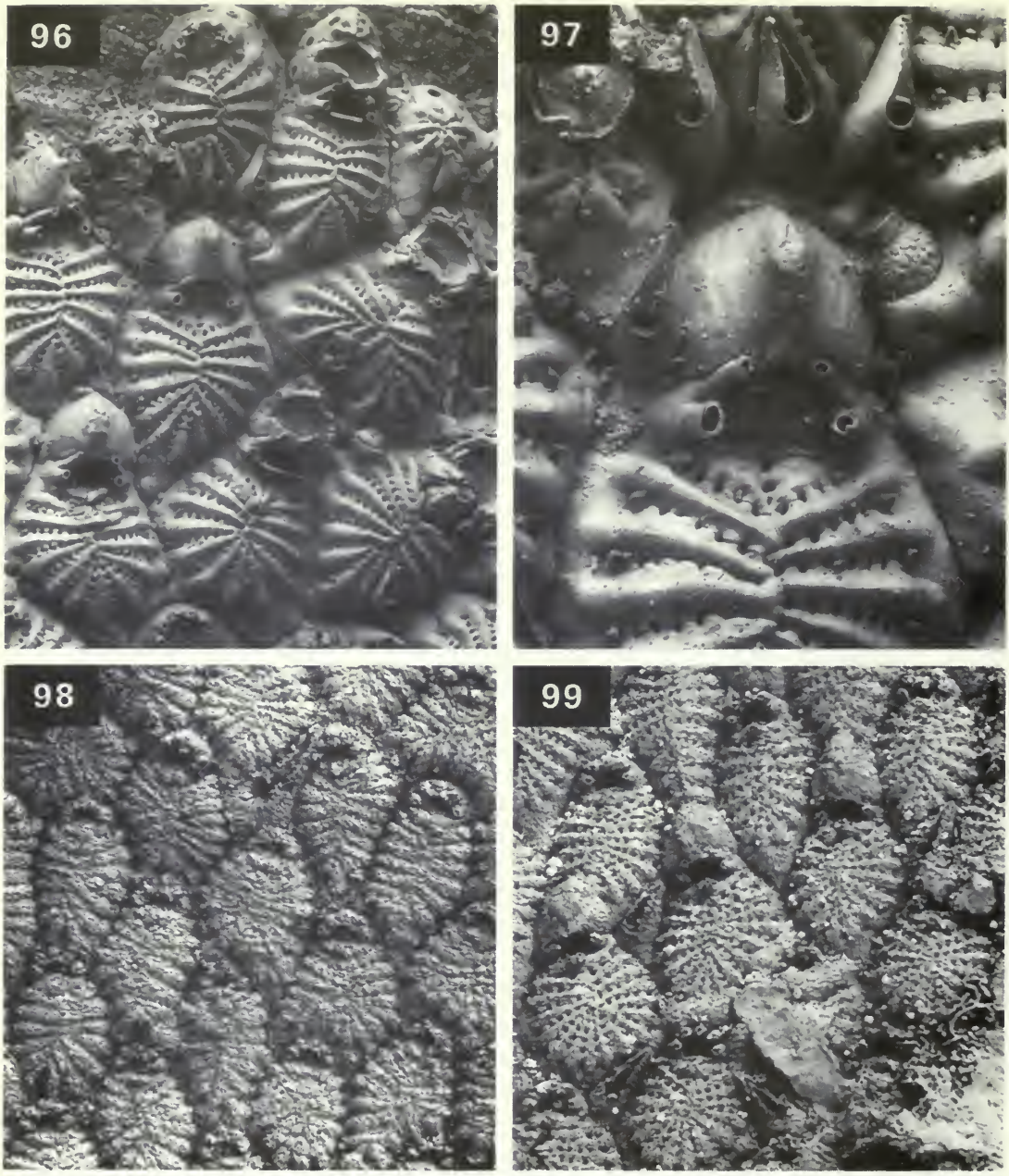
Ancestrula obscured in available material.

Table 13 *Puellina pedunculata* Gautier: measurements in microns

Specimen		Range	Mean	C.V.	n		Range	Mean	C.V.	n
a	Lo	47–50	48·8	2·74	4	Lf	194–233	213	5·51	14
b		40–55	45·2	13·3	5		167–203	187	6·47	12
c		43–46	44·5	5·37	2		199–241	215	5·29	13
a	lo	66–70	67·5	2·73	4	Lfg	230–323	271	9·07	14
b		60–64	61·6	2·86	5		193–297	243	12·4	13
c		63–71	67·0	4·29	6		235–312	266	8·56	10
a	loo	67–80	72·1	5·35	9	lf	168–256	204	10·4	13
b		64–69	66·7	4·09	3		150–187	164	8·55	11
c		69–79	73·7	7·40	3		160–205	175	7·98	13
a	Lov	103–115	109	3·96	9	Lr	66–85	73·0	11·2	6
b		105–118	108	5·46	5		67–77	70·1	5·00	7
c		120–152	132	10·1	6		66–72	68·6	3·99	5
a	lov	115–153	140	7·74	9	Lav	156–158	157	1·01	2
b		126–135	131	2·66	6		—	—	—	0
c		148–160	155	4·48	3		—	—	—	0

a = lectotype (LBIMM-BRY-10384); b = paralectotype (LBIMM-BRY-10384); c = BMNH 1970.6.1.13.

Figs 92–95 (92) *Puellina flabellifera* (Kirkpatrick): part of colony with avicularia, ovicellate and non-ovicellate autozooids, lectotype (BMNH 1888.1.25.10A), Mauritius, × 74; (93) *P. flabellifera* (Kirkpatrick): avicularia (mandibles damaged) and non-ovicellate autozooids, lectotype, × 145; (94) *Puellina minima* (Harmelin): autozooid with category B ovicell and non-ovicellate autozooid at edge of colony, type series (LBIMM), Cassis, France, × 118; (95) *Puellina pedunculata* Gautier: category B ovicell with distal avicularium, BMNH 1970.6.1.13, Marseille, × 280.



Figs 96–99 (96) *Puellina pedunculata* Gautier: part of colony with avicularia, kenozooids, ovicellate and non-ovicellate autozooids, lectotype (LBIMM–BRY–10384), Marseille, ×87; (97) *Puellina pedunculata* Gautier: distal part of autozooid with category B ovicell (kenozooidal frontal shield largely obscured) and avicularia, lectotype, ×220; (98) *Puellina scripta* (Reuss): avicularium (centre, near top) and non-ovicellate autozooids, holotype (NMV 1848/38/75), Badenian, Eisenstadt, ×54; (99) *Puellina venusta* Canu & Bassler: avicularia, ovicellate and non-ovicellate autozooids, BMNH D55588, Badenian, Hartl-lucke, Eisenstadt, ×56.

REMARKS. Three craniid brachiopod valves were sent on loan from LBIMM as substrates of the type series of *P. pedunculata*. One of these was apparently unencrusted, but the other two each bore a colony of *P. pedunculata*. The colony illustrated in Figures 96 and 97 is selected here as lectotype. Neither of the available specimens could be identified as that illustrated by Gautier (1956).

The constant association of the ovicell with an underlying kenozooid in this species does not seem to have been remarked on before. However, a similar arrangement was noted by Harmelin (1978) in his description of the closely related species *Cribrilaria cristata*. Gautier (1956, 1962) and Prenant & Bobin (1966) indicated pores on the ovicell of *P. pedunculata*. These are not in fact present.

Discussion

The use of SEM has been of considerable assistance in the initial discrimination of morphologically similar species of *Puellina*. However, the routine identification of the great majority of colonies of the species dealt with here can be undertaken with a suitable light microscope. Table 14 gives characters by which this may be achieved. Determination of the ovicell category (p. 4) is perhaps the best starting point for an identification.

The present account significantly increases the diversity of *Puellina* known from the British Isles. In the most recent systematic treatment of the British cribrimorph fauna, Hayward & Ryland (1979) recognised four species of *Puellina* and *Cribrilaria*. Of these, *P. setosa* was included only tentatively and is not in fact of proven British occurrence (see above). It is now necessary to add *P. modica* n.sp., *P. praecox* n.sp., *P. bifida, P. arrecta* n.sp. and *P. corbula* n.sp. to the list, although *P. arrecta* qualifies only through a record from Guernsey; a sixth species, *P. directa* n.sp., occurs in the English Channel off Normandy and Brittany but has not so far been recorded from the Channel Isles. *P. arrecta* and *P. corbula* were recorded from the English Channel by Harmelin (1978) as *Cribrilaria flabellifera* and *C. pedunculata* respectively. The record of *C. flabellifera* from the English Channel by d'Hondt (1979) may similarly refer to *P. arrecta*.

Available material of Recent British *Puellina* has a marked southerly and westerly bias, with the North Sea unrepresented. This is probably not entirely a reflection of collection bias. Shell substrates from the western English Channel may have a remarkably high diversity of encrustation, with 6 (BMNH 1985.11.20.69) or 7 (BMNH 1985.11.20.72) species of *Puellina* on a single small shell. All nine of the species reported here from British and adjacent waters may be found in the western English Channel, although *P. gattyae* was not recorded on shell material offshore in this area.

Four species found in British and adjacent waters also occur in the Mediterranean: *P. gattyae, P. venusta, P. arrecta* n.sp. and *P. corbula* n.sp. In addition, *P. innominata* is evidently very closely related to *Cribrilaria innominata* form B in the sense of Harmelin (1970) from the Mediterranean, and *P. bifida* bears considerable resemblance to the Mediterranean species *P. minima* (Harmelin, 1984). *P. modica* n.sp., *P. praecox* n.sp. and *P. directa* n.sp. are not known from the Mediterranean. *P. setosa, P. radiata* (Moll, 1803), *P. cassidainsis* (Harmelin, 1984), *P. pedunculata* Gautier, 1956 and *P. pedunculata* in the sense of Harmelin (1968) (which is considered distinct from Gautier's species) occur in the Mediterranean but have not been found in the vicinity of the British Isles.

Harmelin (1984) treated *Puellina* and *Cribrilaria* as separate genera, and laid particular stress on the form of the ovicell in differentiating between them. Conversely, Gordon (1984) treated *Cribrilaria* as a subgenus of *Puellina*, citing the presence of setiform papillae, a sub-oral lacuna and a pinnate pattern of costae as similarities which outweighed any differences between the two groups. Whilst Gordon's argument is not regarded as conclusive, his arrangement is adopted here, at least in part because difficulties have been encountered with the application of the criterion of ovicell type. Two of the newly described species, *P. praecox* and *P. directa*, have ovicells at variance with their other characters and hence fall between *Puellina* and *Cribrilaria*. Thus *P. praecox* has ovicells of category C (p. 4), yet in many other respects resembles a species of *Cribrilaria*. *P. directa* has ovicells of category A but otherwise, at least superficially, resembles a species of *Puellina*. The

Table 14 Key characters for the identification of *Puellina* from British and adjacent waters. (*Although *P. setosa* is included in this table, its occurrence in the area is unproven.)

	P. gattyae	*P. setosa**	*P. modica*	*P. directa*	*P. praecox*	*P. venusta*	*P. innominata*	*P. bifida*	*P. arrecta*	*P. corbula*
Ovicell type (see p. 4)	C	C	C	A	C	A	A	A (or B)	A	C
Median umbo of costate frontal shield	Variable, none to very large	None or very small	None	None	None	Moderate sub-oral mucro	Large	None	Very large	None
Relief of costate frontal shield	Slightly to strongly convex	Almost flat to slightly convex	Moderately convex	Strongly convex	Edges steep; centre slightly convex	Edges steep; centre slightly convex	Edges steep; centre slightly convex	Edges steep; centre slightly convex	Strongly convex	Edges steep; centre almost flat
Costae: usual number (range)	7 or 8 (5–9)	9 or 10 (7–12)	5 (4–6)	7 or 8 (7–10)	8 to 10 (8–10)	15 to 18 (12–23)	11 or 12 (9–14)	7 to 9 (6–11)	8 or 9 (7–10)	10 to 12 (9–14)
Ornamentation of costa	None	None	Strong ridge, higher towards edge of shield	Strong ridge often higher towards centre of shield	Ridge, higher towards edge of shield	None	Ridge (variable) and/or tubercle near edge of shield	Ridge, higher towards edge of shield	Ridge and/or tubercle near edge of shield	Tubercle or short ridge near edge of shield
Proximal gymnocyst	Broad	Broad	Broad	Broad	Narrow	None or very narrow	Narrow or moderate	Narrow or moderate	Narrow or moderate	Variable, generally moderate
Oral spines (non-ovicellate)	5	5	5	5	5	5	5	5	6	7
Oral spines (ovicellate)	2	2	2	2	4	4	4	4	4	4
External windows of pore chambers	Small	Small	Small	Variable, generally small	Small	Large	Large	Large	Moderate	Moderate
Avicularium	None	None	None	None	None	Frequent	Infrequent to fairly frequent	Infrequent	Frequent	Infrequent to fairly frequent
Additional comments	Single, round intercostal pore (plus 1 papilla pore) between successive costae	First pair of costae slightly more prominent than rest	Prominent costae converge to single point	Distal pairs of costae arranged in parallel lines	Lightly calcified colonies of very few zooids	Most distal intercostal pores largest	Sub-oral lacuna large	Costal ridges often stepped in height	Avicularium with distinctive palate and mandible	Avicularium minute, semi-erect. No setiform papillae

occurrence in *P. bifida* and *P. minima* of ovicells of categories A and B in the same colony, and the evident resemblance of *P. praecox* to *P. bifida*, suggests that the conversion of one ovicell type into another may not be a particularly difficult evolutionary step. It is possible to envisage the transformation of category A into category B by the development of a distal kenozooid rather than an autozooid. Reduction in the size of the kenozooidal costate frontal shield until none was retained would then yield category C (in which the ovicell would nevertheless be regarded as kenozooidal in nature). Such a transformation of category A through B to C, which is considerably easier to envisage than the reverse pathway, may have occurred more than once within the *Puellina* clade. If so, the category C pattern of ovicell development would be a homoplasous character within the genus.

In most species with ovicells of category A, ontogenetically complete maternal autozooids are commonly seen on the edge of the colony before the budding of the distal autozooid with proximal ovicell commences. In this condition, maternal autozooids may be recognised by their reduced number of oral spines (compared with non-maternal autozooids) which are closely spaced near the proximo-lateral corners of the orifice, and by the large U-shaped distal pore (? pore chamber window) in place of the smaller sub-oval pore chamber window(s) of non-maternal zooids (Figs 48, 55, 66 and 79). It may therefore be inferred that there is a distinct pause between the development of the maternal zooid and its corresponding ovicell, caused by the discontinuous growth of the colony. Although it is perhaps more usual for an ovicell of category A to be produced just one autozooid generation after the maternal zooid, a delay greater than one autozooid generation may be inferred in some cases. For instance in Figure 79, zooid 1 is a maternal zooid which contributed to the budding of completed zooid 2, and both 1 and 2 are contributing to the budding of 3. The ovicell within which an embryo produced by zooid 1 would be brooded is not yet fully developed, being a proximal component of zooid 3, two autozooid generations later than 1. It is apparent that the U-shaped distal pore (? pore chamber window) of the maternal zooid is responsible for the production of an ovicell during the budding of a later zooid, so that the ovicell always lies immediately distal to the orifice of the maternal zooid. If the maternal zooid is involved in the budding of more than one subsequent zooid, it is the daughter zooid to which the U-shaped distal pore contributes that bears the ovicell. Thus in Figure 79 maternal zooid 1 has contributed to the budding of zooid 2 through one or more distolateral pore chambers and to the budding of zooid 3 through the U-shaped distal pore; accordingly, the ovicell is part of zooid 3. Although the ovicell usually lies at the proximal end of the distal zooid in a more or less median position, it may be displaced some distance from the proximal end and lie to one side or other of the frontal shield if the spatial packing of the zooids dictates this (compare the two ovicells in Figure 43).

In species with ovicells of category C, ontogenetically complete maternal autozooids are rarely if ever seen on the edge of the colony without a developing or complete ovicell. Thus any pause between the development of the maternal autozooid and the ovicell must be very short, and the process of budding of the autozooid and ovicell is more or less integrated. In this way ovicells of category C are produced earlier, in terms of autozooid generations, than those of category A, and brooding may presumably commence correspondingly sooner.

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The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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Notes on Atlantic and other Asteroidea. 5. Echinasteridae

Ailsa M. Clark*

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Introduction

In the course of reviewing the asteroids of the Atlantic, deciding on the best subdivision of the taxonomically difficult family Echinasteridae has posed numerous problems. Echinasterids are very variable and tend to diversity into local forms, some of them sufficiently well marked and constant to be worthy of recognition as named taxa. Instances of this are provided by Fisher (1911), Hayashi (1940) and Dyakonov (1950) when dealing with the asteroids of three overlapping areas: the whole North Pacific, the vicinity of Japan and the USSR. The three of them described respectively: 8 species and 5 subspecies, of which 9 were new, 17 species of which 10 were new and 19 species with 8 new, all in the genus *Henricia*. With regard to the various Atlantic taxa, Dr F. Jensenius Madsen (pers. comm.) has recently undertaken a revision of the genus *Henricia* in connection with the series 'Marine Invertebrates of Scandinavia' but this still leaves *Echinaster*, which is well represented in the western tropical Atlantic, to be reassessed.

The present study is based partly on examination of the relevant types and partly on a large collection from the *Pillsbury, Gerda, Oregon* and other vessels. The taxa of *Echinaster (Othilia)* are the main concern, especially two new species now described, but one new species of *Henricia* is also distinguished. Diagnoses for *Echinaster (Echinaster)* and *Echinaster (Othilia)* are given and a tabular key is provided to the Atlantic species of *Echinaster*, utilizing both old and newly recognized characters now thought to be of taxonomic significance.

Because of superficial similarities between species, it must be emphasized that few reliable conclusions can be reached about the identity of most echinasterids without first removing the skin from an arm with bleach to reveal the precise form and arrangement of the underlying skeletal plates. In the case of *Henricia*, preparations of the spinelets are also invaluable.

Systematic Account

Family ECHINASTERIDAE Verrill

Echinasteridae Verrill, 1870: 343; Fisher, 1911: 258–260; Downey, 1973: 82–83; Clark & Courtman-Stock, 1976: 88.

Only three genus-group names are involved in the Atlantic fauna, namely *Echinaster* Müller & Troschel, 1840, *Henricia* Gray, 1840 and *Othilia* Gray, 1840. The main problem is the status of *Othilia* which was revived as a distinct genus from the synonymy of *Echinaster* Müller & Troschel, 1840, by Tortonese & Downey (1977) on the basis of the presence of patches of crystal bodies (or glassy tubercles) on many of the primary plates in the type species of *Othilia, Asterias echinophora* Lamarck, 1816. Such structures have not been observed in *Asterias sepositа* Retzius, 1783, the type species of *Echinaster* (see Tortonese & Madsen, 1978). Unfortunately, discovery by Clark & Tortonese (1986) that specimens from West Africa considered to be only subspecifically distinct from *E. sepositus* also have patches of crystal bodies, though ill-defined and restricted to some proximal plates, devalues this character as being of generic weight. However, there is support from two other characters which could be of generic or, at least, subgeneric weight. Firstly, the consistent enlargement to some degree of the primary carinal and adradial series of dorsolateral abactinal plates so as to frame two distinct alternating longitudinal series of skeletal meshes along the median part of each arm, coupled with further longitudinal arrangement of abradial dorso-

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laterals with transverse links between the adradials and the superomarginals. This is restricted to the species included in *Othilia*. Although *Echinaster callosus* von Marenzeller from the Indo-West Pacific has large, longitudinally arranged adradial plates, these are linked by diagonal chains of plates and the carinals are not linked in a continuous series. *E. callosus* probably merits supra-specific distinction for itself but that is beyond the scope of the present study. *E. sepositus* and the other species of *Echinaster* have an irregular reticulum of finer abactinal plates, though in some individuals the abradial plating may tend to form oblique longitudinal and short transverse lines converging on the superomarginal series. Only *E. modestus* Perrier from the west tropical Atlantic may show some enlarged adradial meshes on the proximal half of the arm suggesting the condition found in the species of *Othilia*. Secondly, there is a complete absence of actinal plates in all the species of *Othilia,* the inferomarginals bordering directly on the adambulacrals. (A superficial appearance of supposed actinal spines in some individuals is due to development of isolated spines on either the adradial ends of inferomarginals or the abradial ends of adambulacrals.) In *E. sepositus* and *E. modestus* at least one partial series of actinal plates is developed proximally. However, it must be mentioned that some non-Atlantic species currently included in *Echinaster* also lack actinal plates. Pending a full review of all of these, it seems best to treat *Othilia* as a subgenus of *Echinaster*.

Among the more useful specific characters of this subgenus now recognized are some resulting from differential development of the secondary abactinal plates developed between the adradials and the superomarginals during increase in girth of the arms—namely the abradial plates (Figs 1a,b, 3A,B). In most species of *Echinaster (Othilia)* transverse series of abradial plates initially formed are subsequently linked longitudinally or obliquely by elongate plates and it is usually these that come to bear the abradial spines. However, in some cases the spines are borne preferentially on the transverse plates. Another important character is provided by the nature of the articulations between the two kinds of plates. Usually the longitudinal ones are superimposed on the transverse plates and stand out to some extent, especially medially if the area bearing the spine is swollen, but sometimes the plating is integrated so that the longitudinal plates lie between the transverse bars flush with the surface. Surprisingly, a convex madreporite proved to be consistent throughout a wide geographical range in one new species. The shape and armament of this unique plate may be significant to a lesser extent. Campbell & Turner (1984) have also utilized the regularity of the gyri as a specific character.

ECHINASTER (ECHINASTER) Müller & Troschel

Echinaster Müller & Troschel, 1840: 102; Tortonese & Downey, 1977: 829–830,
Rhopia Gray, 1840: 281.
Verrillaster Downey, 1973: 89.

TYPE SPECIES. *Asterias seposita* Retzius, 1783, by subsequent designation by Fisher, 1913 under the name of *Asterias sagena* Retzius, 1805; validation of *A. seposita* by Tortonese & Madsen, 1979.

A subgenus of *Echinaster* in which the primary abactinal skeleton is not distinct; the plating forms an irregular reticulum medially, though sometimes resolves itself abradially into oblique longitudinal and nearly transverse lines meeting the superomarginal series; few species have a marked distinction between primary and secondary plates. The armament consists of small, usually blunt, slightly spaced spines, most often 0·75–1·0 mm long, rarely exceeding 1·5 mm; these may be limited to the nodal plates. The surface of the plates is usually smooth but exceptionally the matrix of certain proximal plates shows small inconspicuous areas of well embedded crystal bodies, usually only distinguishable when denuded. The marginal plates are in fairly regular rows and more or less enlarged in comparison with the abactinal plates, though never conspicuous. Both series are mainly aligned below the ambitus or widest past of the arm but interradially the early supermarginals may be displaced upwards to some extent if the wedge of intermarginals is widened. The inferomarginals are separated from the adambulacrals proximally at least in the Atlantic species, by at least one partial series of actinal plates. Most of the adambulacral spines are aligned in an irregular line transverse to the furrow into which one or more modified spines are inset.

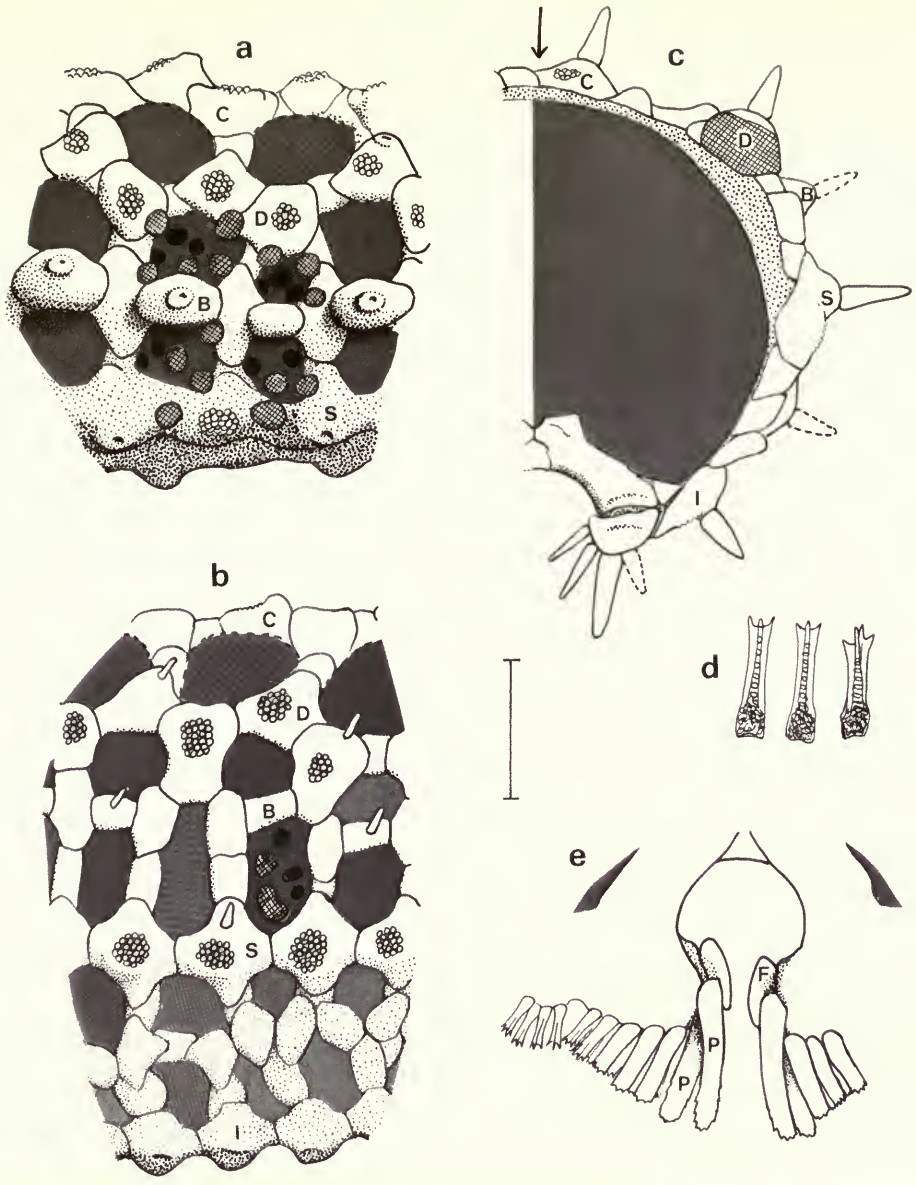

Fig. 1. a. *Echinaster (Othilia) guyanensis* sp. nov. Holotype. Lateral but slightly dorsal view of proximal part of arm (interradius to left) showing some carinal plates in profile (C), adradials (D), transverse and superimposed abradials (B) and superomarginals (S). b. *E. (O). paucispinus* sp. nov. Holotype. Lateral view, letters as in (a) with addition of inferomarginals (I). Glands (cross-hatched) and papular pores (black) shown in only a few areas. c. *E. (O.) sentus* (Say) half cross-section of proximal part of arm, plates lettered as in (a) and (b), the carinal shown offset from midline (arrowed), the adradial partly in section (cross-hatched), spines behind the plane of section shown by discontinuous lines. d,e. *Echinaster (Echinaster) downeyae* sp. nov. *Gerda* st. 311: d. abactinal spinelets, e. cross-section through furrow showing inset furrow spines (F) of two opposite adambulacral plates with a pair (P,P) of larger slightly inset spines, one behind the other, superficial adambulacral spines and also (on left only) actinal spinelets (A) of one plate, sutures omitted. The scale = 2 mm for a–c, 0·25 mm for d, 0·5 mm for e.

ECHINASTER (OTHILIA) Gray

Othilia Gray, 1840: 281; Fisher, 1911: 260 (in key), 261; Tortonese & Downey, 1977: 830.
Echinaster: Verrill, 1915: 35–36; Downey, 1973: 85–86; Walenkamp, 1976: 17–18; de Avila-Pires, 1983: 431–436.

TYPE SPECIES. *Asterias spinosa* Retzius, 1805, non Pennant, 1777, = *A. echinophora* Lamarck, 1816, by subsequent designation by Fisher, 1911.

A subgenus of *Echinaster* in which the primary abactinal skeleton is distinct or even conspicuous in adult specimens, there being a pentagon of linked primary radials and interradials on the disc around the anal area and a large pentagonal or triangular midradial skeletal mesh distal to each primary radial opposite the base of each arm; this is followed along the arm by two series of alternating adradial meshes delimited by the median longitudinal carinal series of plates with an adradial series of dorsolateral plates each side. These primary nodal plates are often linked by one or more secondary intercalary plates in adults, enlarging the meshes; other secondaries link the adradials to the superomarginals, the abradial meshes being usually smaller and subdivided by a distally incomplete longitudinal series of elongate secondary abradials; there is sometimes also a shorter second abradial series in very large specimens ($R > c.$ 60 mm) of some species, or else a longitudinal series is lacking in others where the abradial meshes are broad rectangular. The armament ranges from single large spines on some nodal primary plates, exceeding 1·5 mm in length, to smaller spaced spines or coarse spinelets on most plates including the intercalaries, sometimes multiple on some primaries; the spines of the abactinal and marginal plates form more or less regular longitudinal series totalling 7–13, most often 11. Patches of crystal bodies (glassy tubercles) are embedded in the matrix of many larger plates, especially primaries, and are visible when denuded (or dried unless the skin is very thick); the patches are occasionally reduced in extent or absent, especially when there are large single spines. The marginal plates are in regular horizontal rows, slightly enlarged, usually rhombic; the superomarginals are aligned at or just below half the height of the arm, along the ambitus or widest part of the circumference, but diverge from the inferomarginal series basally when the intermarginal plating is well developed; the inferomarginals are aligned ventrally and are contiguous with the adambulacrals throughout their extent, actinal plates being completely absent; the two inferomarginal series of adjacent rays meet interradially distal to the oral plates with usually a single interradial plate. The adambulacral spines are few and coarse, tending to be aligned in an irregular row transverse to the furrow; one or sometimes two or three spines are inset on to the furrow face of the plate, the innermost at least reduced in size, compressed and curved.

Echinaster (Othilia) guyanensis sp. nov.
Figs 1a, 2A,B

Echinaster sentus: John & Clark, 1954: 140 (listed). [Non *E. sentus* (Say, 1825)].
?*Echinaster echinophorus*: Cherbonnier, 1959: 171–172, fig. 3C,D; ?Zoppi de Roa, 1967: 281. [Non *E. echinophorus* (Lamarck, 1816)]
Echinaster brasiliensis: Downey, 1973: 88, pl. 42, figs C,D; Walenkamp, 1976: 78–81, pl. 18, figs 3,4; 1979: 72–74, pl. 15, figs 1–4, pl. 16, figs 1–4. [Non *E. brasiliensis* Müller & Troschel, 1842].

MATERIAL. *Oregon* st. 4190, 05°48′N, 52°53′W, off French Guyana (Guiana), 45 m, holotype (USNM). Also from numerous other *Oregon* and *Pillsbury* stations between Honduras and the Guyanas as well as in offshore parts of the Caribbean from Pedro Cays, S of Jamaica and from S of Haiti. The westernmost record is from the SW side of Cape Tres Puntas, Guatemala, collected by D. Nestor, via Professor T. Hopkins.

HOLOTYPE. R/r 40/9 mm = 4·4/1; Br/br (proximal breadth to distal breadth measured at 10% R from tip) 10·0/5·0 mm = 2·0/1; R/br = 8·0/1.

The five arms are fairly broad, even at the tip, somewhat tapering in the distal half, appearing rather flattened; the skin is thick enough to obscure the details of the plating but not the regular pattern; the primary pentagon on the disc is conspicuous, also the primary adradial skeletal meshes

alternating along the arms. The plate area is approximately equal to the mesh area. Some intercalary secondary plates link the nodal primaries both longitudinally and transversely. The adradials are linked to the superomarginals laterally by chains of one to three transverse plates on which are superimposed a well-developed, almost continuous, longitudinal series of elongate abradial plates, extending nearly to the tip of the arm, most of them convex medially, while 14 of those on one side of the arm which was cleaned bear an abradial spine. None of these secondary abradials bears a patch of crystal bodies (or glassy tubercles) in contrast to many of the primary carinals and adradials on which the patches usually extend for about half the exposed area of the plate. Carinal spines are fairly well developed but are reduced or absent on some nodal plates; spines are better developed on the adradials, numbering 12–14 in a longitudinal series. All these spinose primaries have the spine mounted on a rounded elevation, the larger ones inset from the distal end of the plate. The spines are single, conical, taper to a point and measure up to 1·5 mm long. The larger proximal adradial skeletal meshes include *c.* 6 papulae and 8–10 dermal glands.

The superomarginal plate series is aligned just below half the height of the arm and the plates are rhombic in shape. They number *c.* 27 on one side of the arm cleaned; of these *c.* 15 bear a single upper or median spine and have smaller patches of crystal bodies than the spineless plates which usually alternate with them. The distal spines are inconspicuous but the more proximal ones are the largest of all the spines. Intermarginal plating is restricted to the base of the arm and there are few intermarginal spines. Thus the number of longitudinal spine series on one arm is 9 rather than the more usual 11 of this subgenus, that is one carinal and two each of adradial, abradial, supero- and inferomarginals. The inferomarginal plates number *c.* 36, of which 29 have spines in one series, only sporadic plates being spineless. Actinal plates are lacking, the inferomarginals abutting directly on to the adambulacrals. Most adambulacrals bear 4 spines of which two are inset into the furrow but there may be an occasional fifth spine either at the abradial (lateral) end or slightly inset into the furrow, especially on some proximal plates. The spines form a fairly straight transverse row and are webbed together. Most of the oral plates bear 3 marginal spines and one suboral; there are probably also a few inset spines near the distal end hidden in the furrow.

The madreporite is 2·7 mm in diameter and almost circular; it is very unusual for an *Echinaster* in being distinctly convex; the fairly straight ridges which separate the gyri are studded with spinules all along their lengths.

Other specimens. The maximum R is 67 mm; R/r ranges from 4·1–4·9/1, mean 4·5/1 in 14 specimens with R > 30 mm; R/br ranges from 8·0–12·0/1, the degree of taper being rather varied and the arms narrower at the tips in some specimens. The primary skeleton is always fairly regular and conspicuous, the meshes showing dark in contrast in the dried specimens. The reticulum may be more delicate and open than in the holotype and some of the meshes may be partially confluent. The frequency of the spines and their size is often least on the carinal series but both increase towards the superomarginals. The size of the patches of crystal bodies often exceeds half the exposed area of those primary plates that bear them, the patches in the holotype being smaller than usual. The number of adambulacral spines is usually 5 on most plates of the proximal half of the arm, sometimes even 6, with 3 spines often inset into the furrow.

Discussion. Out of a total of > 150 specimens taken between Guatemala and French Guyana, only four have R > 50 mm. The distinctly convex madreporite appears to be an almost constant feature, only three specimens studied having the plate virtually flat. The body form with arms appearing slightly flattened and more tapering distally is also remarkably consistent in the material as dried. The main variations are the relative coarseness of the reticulum and the degree of development of the spines. There seems to be some local tendency in one direction or another, for instance in Venezuelan specimens the skeleton seems to be unusually delicate and the spines smaller. Further to this, the collection of the British Museum (Natural History) includes three very old specimens from Puerto Cabello, W of Caracas, Venezuela (*c.* 68°W), at least two of them collected by Brandt, the third coming via the Wyville Thomson collection and possibly also from the same source, collectors in this area of South America prior to 1850 being few. These specimens have a very delicate, almost lacelike, reticulum, a few plates in the abradial areas being longitudinally aligned and slightly superimposed; no spines or articulations for spines can be seen (though admittedly the

Table 1. Tabular key to the Atlantic species of *Echinaster (Othilia)* above and *Echinaster (Echinaster)* below the line

	1	2	3	4	5	6	7	8		9
echinophorus	20–57	3·5–4·8/4·4	c	E F	r ua	C	7(9)	SP	C	c
guyanensis	29–67	4·1–4·9/4·5	bn	O C	r u	C	9(11)	SP	I(D)(C)	n(i)
sentus	27–63	3·8–4·8/4·4	b(c)	OE F	r ux	O	11	SP	IC	n
spinulosus	35–90	4·1–5·9/5·0	ns	O F	r x	D(C)	11	S(O)B(P)	D	i
graminicola	15–27	3·3	b=c	O F	i p	C	9(11)	SB	D	i
serpentarius	41,48	4·8, 5·3	s(?b)	E F	i a	C*	11	MB	D	i
brasiliensis	35–66	4·5–5·3/4·8	b	O F	ri ax	C	9–11	S(M)B	I,D	n
paucispinus	38–63	4·5–5·8/5·3	n(sb)	O F	r x(u)	C	11(12)	SB	D	d(i)
sepositus	50–90	5·0–8·0/6·5	db(a)	O F	(r) p	N	X	SOB	I	n
sep. madseni	44–80	6·8, 7·1	a(n)	O F	(r) p	N	X	SO(B)	I	i
modestus	33–78	4·0–6·1/4·9	sa(c)	E F	r p	J*	X	O(S)B(P)	I	i
reticulatus	c.70	4·7, 5·0	c	O F	(r) p	N	X	S(O)P	—	i

1. Range of R in specimens examined:

2. Range and mean of R/r:

3. Shape of arms (of limited use because of variability);
   - c—short, stout, cylindrical, only slightly tapering.
   - d—digitate, relatively long and fingerlike, fairly broad at tips, br (breadth at 10%R from tip) usually 5–7 mm at R *c.* 40 mm.
   - b—broad throughout but slightly tapering, tips still fairly broad (Fig. 2A).
   - n—tapering evenly but markedly to fairly narrow tips, br 2·5–5·0 mm (Fig. 2C).
   - s—slender, tapering more basally than beyond.
   - a—long and tapering to attenuated tips.

4. Shape of madreporite:
   - O—almost circular.
   - E—distinctly elongate, interradial diameter at least 1·25 × tangential diameter.
   - C—surface convex.
   - F—surface flat or slightly concave.

5. Surface of madreporite:
   - p—with peripheral encircling spinules only.
   - a—with additional spinules near the periphery.
   - x—with extra spinules even centrally but peripheral ones larger.
   - u—with uniform spinules all over the ridges, or peripheral ones appearing smaller.
   - i—gyri irregular.
   - r—gyri radiating fairly regularly, separated by almost straight ridges.

6. Distinctness of primary pentagon outlining anal area on disc and of enlarged double series of primary adradial skeletal meshes along arms, at least in intact dried specimens.
   - C—conspicuous (Fig. 2A,C).
   - D—distinct.
   - J—the proximal adradial meshes at least on arms just distinguishable.
   - O—obscured by thick skin.
   - N—no distinct longitudinal arrangement.
   - *—pattern not or less distinct on disc than on arms.

7. Number of longitudinal series of abactinal and marginal plates or spines proximally: i.e. carinals, adradial and abradial dorsolateral, supero-, inter- and inferomarginals (multiple marginal spines counted as one; this is an odd number unless the carinal series is so zig-zag as to appear as two series).
   - X—only limited longitudinal arrangement or complete irregularity.

8. Abactinal spines: number, shape and alignment:
   - M—multiple on all or most plates.
   - O—often multiple but with rarely more than two spines on one plate.
   - S—predominantly or entirely single.
   - P—pointed.
   - B—blunt, often bullet shaped.
   - C—arising from apex of large convexity.
   - I—inset from distal end, sometimes central, convexity smaller.
   - D—arising near distal edge of plate from only a minimal elevation (spine often appressed distally in preservation).

9. Abactinal and superomarginal spines: size at R 40–50 mm, largest spines only.
   - c—conspicuous, at least 1·5 mm.
   - n—noticeable, 1·1–1·4 mm.
   - i—inconspicuous, 0·75–1·0 mm.
   - d—diminutive, *c.* 0·5 mm.

10. Crystal bodies (glassy tubercles): occurrence and patch size.
   - +/−—present or absent.
   - e—extending over at least half the exposed area of many primary plates.
   - r—restricted to compact patches less than half the plate area (Fig. 1a,b).
   - f—few and appearing deeply inset in the matrix or eroded, in very small patches.

10	11	12	13	14	15	16	17	18
+ r(c)	>(=)	U(S)	a(1)	15–27/30–65	R	o	3(4) 0 2(1)	T
+ e(r)	<=>	S	l	22–36/31–73	R	o	4,5 0 3,2	T
+ r(f)	>	M(S)	pl	24–35/47–82	E(R)	o	3(4) 0 2(1)	T(O)
+ e(r)	>	S	l	30–48/87–100	E	o	4(3) 1 1	O
+ e	>	S	l	20–23/c.73	(E)	o	2,3 0(1) 1	—
+ r	=	S	l	— —	E	o	5,4 0 2(1)	T
+ r	<	F	t(a)	22–32/61–100	E	o	5,4 0 1(2)	T
+ r	<(=)	F	lo	29–40/73–97	E	o	4(3,5) 0,1 2	T(O)
— —	>	R(O)	u	— —	R	s,m	3(2) 0 1	T
+ f	>	R	u	— —	R	s,m	3 0 1	T
— —	>	R(O)	u	— —	R(E)	m	5(4–7) 1 2(1)	(T)
— —	=?	R	u	— —	R	s	3(4) 0 1	?

11. Area of proximal primary abactinal plates relative to adradial mesh area (estimated approximately by eye).
    >—greater.
    =—equal.
    <—less.

12. Abradial dorsolateral plating:
    U—undeveloped, only short series of one or two intercalary plates linking adradials with superomarginals.
    F—more extensive, all plates nearly flush with the surface, consisting of chains of transverse rectangular plates, sometimes bifurcating, often linked by oblique or longitudinal plates set between the transverse ones, that is integrated with them, all these plates lacking patches of crystal bodies (Fig. 1B).
    S—consisting of longitudinal elongate and more or less convex spinose plates standing out from the surface, their ends being superimposed on the transverse chains, often forming continuous longitudinal series (Fig. 1a).
    M—of mixed form, some plates becoming modified into polygonal shapes with the addition of extra lobes and sometimes also developing a patch of crystal bodies or bearing a spine, though other proximal ones are elongate and superimposed while distal ones are all polygonal with crystal bodies, resembling the adradial plates.
    O—tending to form oblique linear series towards the superomarginals, sometimes forming a partial trelliswork.
    R—forming an irregular reticulum without consistent linear arrangement.

13. Abradial dorsolateral spines:
    a—absent or few, limited to arm bases.
    l—all or most on longitudinally-aligned or oblique plates.
    p—all or most on polygonal plates.
    t—all or most on transverse plates, even if oblique or longitudinal plates are present.
    o—all on transverse plates, which are the only ones present.
    u—uniformly on most abradial plates.

14. Spinose superomarginal plates: total number of plates in series and percentage with a main upper or distally middle spine at R 40–60 mm.

15. Occurrence of intermarginal plates:
    E—extending beyond half the arm length (measured laterally from interradius to arm tip).
    R—restricted to less than half the arm length.

16. Actinal plates:
    m—in multiple series proximally.
    s—in a single series, even on disc.
    o—lacking altogether, inferomarginals contiguous with adambulacrals throughout (note that isolated lower inferomarginal spines or lateral adambulacral ones may simulate actinal spines.

17. Adambulacral spines: total number on one plate; number on abradial or 'subambulacral' part of the plate; number inset into furrow and appearing smaller than the main furrow margin spine, its tip at a higher level.

18. Arrangement of adambulacral spines:
    T—in a transverse, almost straight series, though the spine following the main furrow margin spine may have its tip aligned distally.
    O—this same spine more obviously offset distally.

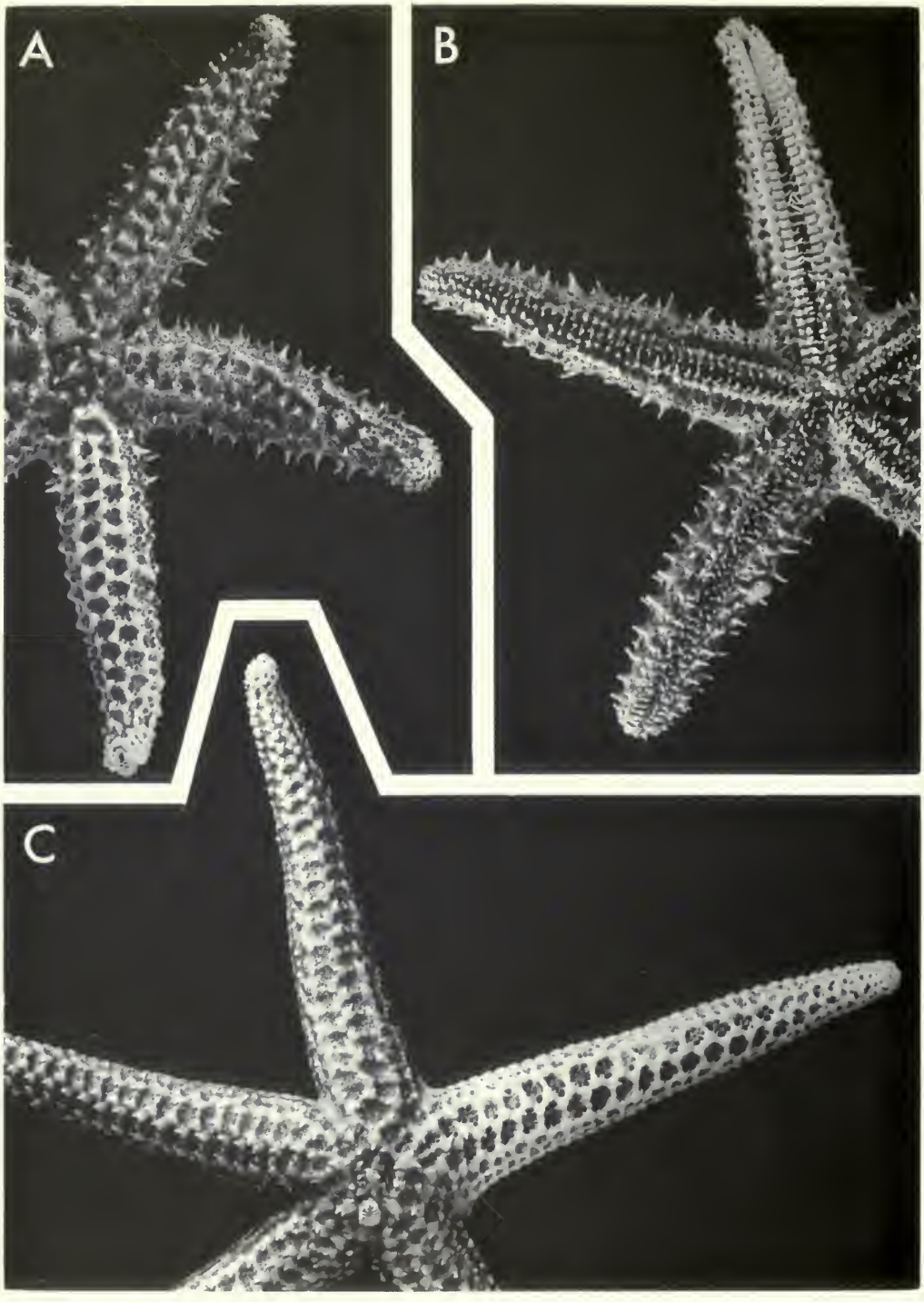

Fig. 2. A. B. *Echinaster (Othilia) guyanensis* sp. nov. *C. E. (O.) paucispinus* sp. nov. Holotypes. All × 1·5.

preservation is poor). Thomson gave his specimen an MS name derived from the last character but further material from the area is needed to establish if such an extreme variant still exists. Unfortunately, all Zoppo de Roa's Venezuelan samples (1967) appear to be from localities east of Caracas or from offshore islands to the north and east. She referred her specimens to *E. echinophorus* and described them as having prominent spines ('espinulas conspicuas') 1 + mm long in 7–9 series; they were commonly found among mangroves at 1·5 m. Surprisingly, despite abundant collections, neither Engel (1939) nor Ummels (1963) recorded any specimens of *Echinaster* from the Netherlands Antilles to the north of Venezuela.

On the northern coast of Brazil to the east of the Amazon outflow, which might form an ecological barrier, a few other specimens of *Echinaster* were taken by the *Oregon* which resemble *E. guyanensis* in some characters but are otherwise more like *E. echinophorus,* the common species on the east coast of Brazil north of *c.* 20°S. The taxonomic status of these specimens is uncertain; they will be discussed further by Clark & Downey (in prep).

The fact that such a common species of *Echinaster* with a fairly wide geographical range has previously escaped recognition can be attributed not only to the confusion as to specific limits in the genus in the tropical west Atlantic which has prevailed, but also to the superficial resemblance between *E. guyanensis* and *E. brasiliensis,* which latter species was only recently shown by de Avila Pires (1982), in a fine review of *Echinaster* in Brazil, to be limited in that country to the southern half, giving way to *E. echinophorus* in the northern part of the east coast. Due to lack of material, she was unable to establish the specific identity of any specimens from the north coast of Brazil.

RANGE. From Guatemala east and south along the Atlantic coasts of Central America and northern South America, at least to French Guyana, possibly also to westernmost north Brazil; 13–106 m; from coarse calcareous sand; shell gravel; muddy sand; sand and shells; muddy sand and gravel; or 'muddy' or 'sandy' substrates.

Echinaster (Othilia) paucispinus sp. nov.
Figs 1b, 2C, 3A,B

Thyraster serpentarius: Gray, Downey & Cerame-Vivas, 1968, fig. 29 [?non text].
Echinaster sp. B, Downey, 1973: 89, pl. 41, figs C,D.

MATERIAL. Hourglass Project st. D. 27°37′N, 83°58′W, *c.* 65 miles W of Egmont Key, Florida, 55 m, holotype (USNM), paratype (BM(NH) no. 1986.1.2.1) and second paratype (Florida Department of Natural Resources, St Petersburg Reference Collection no. I 6816). Other samples from Hourglass sts E, also W of Egmont Key, 73 m, J, K, L and M, W of Sanibel Island, 18, 37, 55 and 73 m (31 specimens). Also from St Petersburg Laboratory collection: Topsoil Bluff, Walton County, NW Florida, 30°22′N, 86°21·5′W, 12 m (2); off Panama City, NW Florida, 30°05′N, 85°46′W, (5). University of Alabama no. 8114–0157, off Panama City, *c.* 30 m; no. 8114–0147, 28°32′N, 84°19′W, *c.* 30 m; no. 8114–0153, 27°23·5′N, 84°08′W, 85 m (8). Continental Shelf Associates, Inc., via Dr R. Turner, NW of Dry Tortugas, 25°12·9′N, 83°22·7′W, 67 m (1).

HOLOTYPE. R/r 55/5·5 mm = 5·8/1; Br/br (proximal breadth to distal breadth at 10% R from tip) 10·5/4·0 = 2·7/1; R/br = 13·8/1.

The five arms are relatively slender and taper evenly to rounded tips. The skin is thin and the regular pattern of the primary skeleton conspicuous, the meshes appearing dark in dried specimens in contrast to the plates; the meshes appear about equal to the plates in total area but may slightly exceed them. Single secondary intercalary plates link most primary carinals and adradials both longitudinally and transversely on the proximal parts of the arms. The adradials are linked to the superomarginals by short transverse chains of secondary abradial plates some of which are linked longitudinally by other abradials integrated with them, that is inset on the same level, not superimposed. Most of the abradial spines are borne on these longitudinal plates. None of these secondary abradial plates bears a patch of crystal bodies (or glassy tubercles) embedded in the surface matrix, in contrast to nearly all the primary carinals and adradials. These patches are compact and relatively small, occupying less than half the surface area of the plate. This is correlated with the remarkably small size and low frequency of the spines, most of which are little more than 0·5 mm

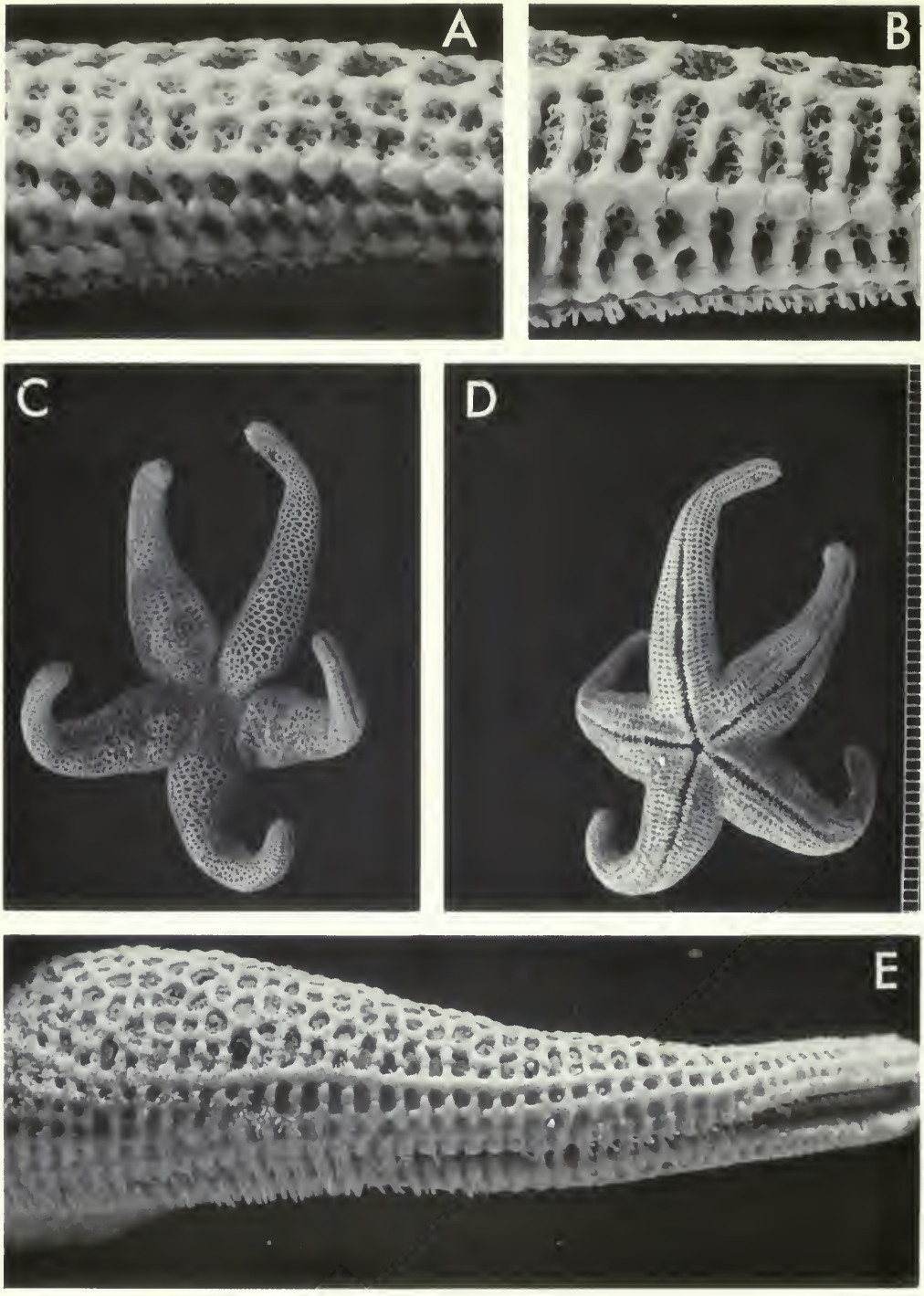

Fig. 3. A, B. *Echinaster (Othilia) paucispinus* sp. nov. Holotype (A) and paratype (B) Lateral views of proximal part of arm. C–E. *Henricia downeyae* sp. nov. Holotype. E. Lateral view of arm. A,B × 4, C,D × 1·5, E × 6.

long; however, they are rubbed and poorly preserved in this specimen; in the paratypes they are tapering and blunt-tipped but still inconspicuous, at most 0·75 mm long, and arise at the distal ends of the plates, except for those on the longitudinal abradials. The larger proximal adradial meshes include a total of *c.* 12 mixed papulae and glands in approximately equal numbers but the number of papulae declines towards the lower surface, only single glands occurring between some inferomarginals and adambulacrals.

The superomarginal plate series is aligned just below half the height of the arm. The individual plates are 4-lobed and mostly contiguous but distally some of them are slightly separated or linked by secondary plates; most bear a diminutive spine just above and distal to the patch of crystal bodies. The intermarginal plating extends for more than half the lateral arm length but is irregular, few plates bearing spines, so that there are only 9 longitudinal series of spines: one carinal and two each of adradial, abradial, supero- and inferomarginals, but all the spines are very inconspicuous. The inferomarginal plates are similar to the superomarginals in shape; on the lower side they are directly contiguous with the adambulacrals, no actinal plates being developed. The adambulacrals bear 4 or occasionally 5 spines of which two are more or less reduced in size and inset into the furrow on most plates of the proximal half of the arm; the abradial part of the plate may bear a spine when there are five but is more often bare.

The madreporite is oval, 2·7 × 2·2 mm, flat and with radiating ridges; the spinules are somewhat rubbed but there appear to be some inset from the periphery in addition to the peripheral ones. The paratype with R *c.* 59 mm probably has the armament intact and shows that spinules are absent from the central part; it has *c.* 15 peripheral spinules.

Other specimens. The paratype just mentioned also has fairly slender arms though the tips are slightly broader. It differs from the holotype mainly in lacking longitudinal abradial plates (Fig. 3B) though a few of the transverse chains of proximally three, distally two, abradials fork; the uppermost (or middle one when three) often bears an abradial spine. The plating of the wide intermarginal areas tends to follow the same pattern as that of the abradial areas and is more regular than in the holotype. Another 'Hourglass' specimen has particularly stout arms, R/r being 51–52/11·5 mm = only 4·5/1, with Br/br 13/6 mm and R/br only 8·5/1.

Discussion. This species resembles most closely *E. brasiliensis* Müller & Troschel, known from the southern half of Brazil and northern Argentina. They share reduced development of longitudinal abradial plates which are integrated, rather than superimposed, when present, coupled with the relatively slender skeletal reticulum and small size of the crystal body patches. However, in *E. brasiliensis* the abradial spines are almost invariably borne on the transverse plates, even when longitudinal or oblique ones are present and the size of these and of all the other spines is considerably greater than in *E. paucispinus*. The two are separated geographically by the ranges of *E. guyanensis* and *E. echinophorus,* the latter being the common *Echinaster (Othilia)* of the northern part of the east coast of Brazil, with sporadic records through the northern Antilles to Nicaragua, while two small specimens have just been recognized from localities in the southern Florida keys, where it overlaps with the common coral reef species *E. (Othilia) sentus* (Say).

Range. The west Florida shelf in the eastern Gulf of Mexico, NW and W of Florida, *c.* 30·5°N, 86·5°W, S to nearly 25°N; 12–85 m; associated with sponges usually in combination with coral, shell, bryozoa, algae, sand or (in one case only) rock.

Henricia downeyae sp. nov.
Figs 1d,e, 3C–E

?Henricia sp. Downey, 1973: 85, pl. 38, figs C,D.

Material. *Pillsbury* st. 1187, 18°17′N, 75°03′W, off Haiti, 1033 m, holotype (USNM). *Gerda* st. 311, 25°44′N, 79°32·5′W, off Miami, Florida, 805–787 m (2 specimens); st. 354, 25°39′N, 79°32′W, 805–832 m (4); st. 830, 25°41·5′N, 79°59′W (1). *Pillsbury* st. 689, 08°14′N, 57°38′W, off Surinam, 1370–1444 m (3). The holotype has R/r 30/7 mm = 4·3/1; Br/br (proximal to distal arm breadths, distal breadth measured at 10% R from tip) 8·0/2·5 mm = 3·2/1.

The five arms are swollen basally constricting the interradii. The abactinal reticulum is fairly open, mesh area exceeding plate area, at least when fully expanded; the plates have 2, 3 or 4 lobes and are similar in size; their contours are simply convex without well defined ridges. The spinelets of the holotype are badly rubbed and incomplete but those of the other specimens, when intact, are consistently mainly trifid with three glassy flanges ending in slightly flared points on about the same level (Fig. 1d); a few spinelets have one or two additional flanges and points; the central perforated core is narrow. The skeletal meshes of the holotype are sunken in drying but a few positive papulae, as distinct from dermal glands, are recognizable.

The superomarginal plates form conspicuous regular horizontal subambital series except interradially where those of the first 3–4 mm run obliquely upwards nearly to the ambitus. Each plate is 4-lobed but the upper lobe is shorter, making the plate appear longer than broad. The upper of the two short intermarginal series has *c.* 12 plates extending for *c.* 7 mm, the lower for only 3 mm on the arm cleaned. The intermarginal meshes are rounded, well defined and similar in shape to the abactinal meshes. The inferomarginal plates resemble the superomarginals in shape but the upper lobes are better developed giving a slightly larger average size.

The actinal plates also have 4 lobes but the adradial one is usually very short or even undeveloped. The area of each just exceeds that of the corresponding inferomarginal. The main (adradial) actinal series extends for *c.* 23 mm or about 2/3 R on the arm cleaned but the distal plates are very small. A second series of *c.* 7 plates extends for 4–8 mm proximally but is occluded interradially by the incurving of the first inferomarginal plates. Distal to the adradial series the rounded meshes or sunken areas continue to the terminal plate between the inferomarginals and the adambulacrals but the single organ in each may be a dermal gland rather than a papula.

The adambulacral plates bear numerous spines about three abreast across the abradial (subambulacral) part of the plate graduated to the several relatively coarse but not much longer spines on the furrow margin. Inset deep in the furrow is a single small spine with 2 (occasionally 3) much larger other spines on about the same level just superficial to it (see Fig. 1e), which were probably initially furrow margin spines but have become inset during growth.

The madreporite is concealed by the folding of the interradii in preservation. The best preserved of the other specimens shows a single madreporite, its irregular ridges covered with scattered spinelets not much smaller than the abactinal spinelets.

Other specimens. These too are relatively small, R up to only 25 mm, R/r 4·7–5·0/1. The best preserved, from *Gerda* st. 311, has R 19 mm; the abactinal reticulum is more compact than in the holotype, the plate and mesh areas being approximately equal; the superomarginal plate series is less distinct than that of the holotype but the inferomarginals are well developed; the intermarginal plates number only about 8 but the main actinal series extends for *c.* 12 mm (over $\frac{1}{2}$ R). There are no skeletal meshes adjacent to the adambulacrals, the only ones on the lower surface being between the inferomarginals and the actinals, but some of these appear to have papulae in them. At this small size and with the dried condition of the material the distinction between papulae and glands is not clear. Breakage of an arm shows that superficial to the deeply inset small curved furrow spine there are two larger spines arising on the same level, one proximal and one distal to it, also somewhat inset but so long that they project further than the next spines which are on the furrow margin itself (Fig. 1e). If these were initially furrow margin spines but have become inset during growth, as seems likely, it is possible that larger specimens with R > 35 mm might have additional spines inset on to the furrow face of some adambulacrals. Downey described 'about six short, stumpy spines' (presumably foreshortened as viewed ventrally) 'roughly in two vertical rows of three each' on the furrow faces of the adambulacrals of the two specimens she designated as '*Henricia* sp.', probably from the larger one, which was from the vicinity of Porto Rico and had R 62 mm. If this specimen is conspecific with the holotype of *H. downeyae,* it would support the theory of adambulacral spines shifting relative to the contours of the plates during growth. However, close scrutiny of the photographic negative of this specimen from which her plate 38C was made has shown that it has two madreporites in spite of only having five arms, while she herself found three madreporites in her smaller specimen from SW of Florida. Accordingly, both of these could be potentially fissiparous and so possibly conspecific not with *H. downeyae* but with the

fissiparous *H. sexradiata* (Perrier), which also has multiple spines inset into the furrow. In a specimen of *H. downeyae* from Surinam with the characteristic trifid spinelets, some of the adambulacral plates have two compressed curved inset furrow spines vertically one above the other and then the next two spines are almost superficial, demonstrating another variation.

AFFINITIES. Although the trifid form of the spinelets in *Henricia downeyae* agrees with that in *H. pertusa* (O. F. Müller) from the bathyal NE Atlantic, as being distinguished by Madsen (pers. comm.), that species has a more simple adambulacral armament with only a single inset spine. There is probably greater affinity with the partly sympatric West Indian *H. sexradiata* (Perrier), which shares the complex furrow armament. *H. sexradiata* differs most obviously in having six or seven arms, coupled with multiple madreporites and a fissiparous habit, also relatively more slender arms. The abactinal reticulum is probably coarser, though this character, like the occurrence of papulae on the lower side, varies in most species of the genus. The spinelets, though mainly glassy in both, have one prolonged point in *H. sexradiata,* approximating in this character to the other West Indian species *H. antillarum* (Perrier), in which the arms are consistently much more attenuated than in *H. downeyae.*

RANGE. From the Florida Strait east and south to Surinam; 342–1370 (?1444) m.

Acknowledgements

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Observations on the marine nematode genus *Spirinia* Gerlach, 1963 (Desmodoridae: Spiriniinae) with descriptions of two new species

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Synopsis

Observations on the nematode genus *Spirinia* Gerlach, 1963 are made including notes on its systematic position. The genus is characterized by the shape of the head, form and position of the amphids, narrow slightly cuticularized buccal cavity, short oesophagus with a pronounced bulb and form of the male genital apparatus. The tail-shape separates the genus into two sub-genera—conical in the subgenus *Spirinia* and flagellate in the subgenus *Perspiria*. A list of the valid species is given together with notes of those considered as *nomina dubia* and a dichotomous key for the determination of species. Descriptions and/or notes are given of the following species: *Spirinia (S.) parasitifera* (Bastian, 1865): *S. (S.) schneideri* (Villot, 1875); *S. (S.) hopperi* sp. nov.; *S. (S.) laevis* (Bastian, 1865); *S. (S.) gerlachi* (Luc & DeConinck, 1959); *S. (Perspiria) hamata* Wieser & Hopper, 1967; *S. (P.) mokii* sp. nov.

Introduction

This report was prompted by a collection of *Spirinia parasitifera* (Bastian, 1865) from localities in North America (Canada; Massachusetts and Florida, USA) provided by Mr Bruce E. Hopper of the Canadian Department of Agriculture. Apart from one population in Nova Scotia (Bras d'Or Lake) they show variation in the form of the manubrium (cephalated proximal portion of the spicule) not apparent in *S. parasitifera* from European waters. As this is the only character in which they differ a taxonomic distinction is not justified. Specimens of *S. parasitifera,* as well as four other species, including one described as new (*S. (S.) hopperi*) from British coasts are also examined. A new species belonging to the subgenus *Perspiria* Wieser & Hopper, 1967 (*S. (P.) mokii*) from Malaysia is described. Observations are also made on specimens of *S. (P.) hamata* Wieser & Hopper, 1967 from Florida.

Typically *Spirinia* species live in sandy and muddy habitats and are often found in sand surrounding the roots of *Zostera* (eelgrass). Twenty-five nominal species have been described, 13 of which are currently included in the genus. See Gerlach & Riemann (1973) for nomenclatorial changes and synonymies up to 1972. Since 1972 another species (*Spirinia (S.) gnaigeri* Ott) has been described from an inter-tidal sand-flat, Bermuda (Ott, 1977).

A list and key to all valid species of *Spirinia* is included (see p. 80). Notes are also given of species considered as *nomina dubia*.

Material and methods

The specimens from British coasts were fixed in formalin with sea-water. All specimens studied are deposited in the collection of the British Museum (Natural History). The examination was carried out mainly with the light microscope using transmitted light interference microscopy in some instances. Specimens of *S. (S.) parasitifera*, *S. (S.) schneideri*, *S. (S.) hopperi* and *S. (S.) laevis* were also examined with a scanning electron microscope for elucidating details of the labial and cephalic sensilla and for the appearance of the cuticle. Only absolute measurements are given (see Tables I–X). The head diameter was taken at the mid-level position of the amphids. Measurements of the arc-length of the spicules are given, not the chord.

Systematic position of *Spirinia*

The genus (as *Spira*) was established by Bastian (1865) but first fully characterized by De Man (1890). As *Spirina* Filipjev, 1918 it was first included in the family Desmodoridae (established as sub-family Desmodorini) by Filipjev (1922), subsequently raised to family by Steiner (1927). Chitwood (1936) subdivided the Desmodoridae into four subfamilies and included *Spirina* in a tribe Spirinacea of the subfamily Richtersiinae and Wieser (1954) followed this classification in a revision of the genus with a key to species.

Gerlach (1963) changed the name *Spirina* Filipjev, 1918 to *Spirinia* because the name *Spirina* was found to be preoccupied by a mollusc. More recently there have been changes in the classification of the Desmodoridae and *Spirinia* is currently placed as the type-genus of the subfamily Spiriniinae. See De Coninck (1965), Gerlach & Murphy (1965), Wieser & Hopper (1967), Gerlach & Riemann (1973) and Lorenzen (1981). Wieser & Hopper (1967) erected the subgenus *Perspiria* for the species of *Spirinia* having a flagellate and coarsely-striated tail.

Spirinia is redefined as follows: Desmodoridae, Spiriniinae. Cuticle with or without transverse striations. Body setae present. Head narrow but not set-off from body, more truncate in some species than in others. Buccal cavity small and narrow, the walls only slightly cuticularized, sometimes with minute teeth. Amphids a prominant single spiral, circular in outline, situated near the anterior end. Oesophagus usually short in comparison with the total body-length (an exception being a species belonging to the subgenus *Perspiria*) and with a posterior bulb. Testis single and straight (outstretched). Spicules paired, arcuate, of equal length, with a club or hook-shaped expansion (manubrium) at the proximal end. Gubernaculum short, without a posteriorly directed apophysis. Ovaries paired and reflexed. Tail conical in the subgenus *Spirinia,* flagellate in the subgenus *Perspiria*.

The closest related genus is *Chromaspirina* Filipjev, 1918, which has a larger and more heavily-cuticularized buccal cavity, often armed with larger teeth than in *Spirinia*. Also the transverse striations are much coarser compared with those in *Spirinia*. Cuticular striations are not present in *S. schneideri* and *S. hopperi*. Lorenzen (1981) has noted the similarity of *Alaimonema* Cobb, 1920 to *Spirinia*. Although Cobb (1920) gives quite a detailed description, the important differential characters are not clear, and there is only an illustration of the anterior end of the worm.

List of valid species of *Spirinia*

Subgenus *Spirinia* sensu stricto Gerlach, 1963

S. (S.) gerlachi (Luc & De Coninck, 1959)
S. (S.) gnaigeri Ott, 1977
S. (S.) hopperi sp. nov.
S. (S.) laevioides Gerlach, 1963
S. (S.) laevis (Bastian, 1865)
S. (S.) parasitifera (Bastian, 1865)
S. (S.) schneideri (Villot, 1875)
S. (S.) septentrionalis (Cobb, 1914)
S. (S.) tenuicauda (Allgén, 1959)

Subgenus *Perspiria* Wieser & Hopper, 1967

S. (P.) flagellata Vitiello, 1971
S. (P.) hamata Wieser & Hopper, 1967
S. (P.) mokii sp. nov.
S. (P.) striaticaudata (Timm, 1962)

Dubious species

Spirinia (S.) sabulicola (Filipjev, 1918) was described from the Black Sea from female specimens only. Males have not been found since and there are no redescriptions, so this species is unlikely to

be recognized with any degree of certainty. It is therefore treated as a *nomen dubium*. *S. (S.) similis* (Cobb, 1898) was described without an illustration and also unlikely to be recognized. It is therefore regarded as a *nomen dubium*.

Key to subgenera and species

1	Tail shape conical, of varying length but never filiform (subgenus *Spirinia*)	2
1′	Tail shape filiform, transverse striations of the cuticle more prominent on the tail (subgenus *Perspiria*)	10
2	Body setae short (up to 10 μm)	3
2′	Body setae long (greater than 10 μm)	7
3	Cuticular striations present	4
3′	Cuticular striations absent	6
4	Striations on the cuticle resolvable into dots	*S. (S.) septentrionalis*
4′	Striations on the cuticle not resolvable into dots	5
5	Amphids about one-third of the corresponding head diameter in width, tail typically conical	*S. (S.) parasitifera*
5′	Amphids 75% of corresponding head diameter in width. Males twice the length (2·12 mm) of the females (1·35 mm), tail uniformly thinner in its posterior part	*S. (S.) tenuicauda*
6	Tail short (1–1·5 times anal body diameter in length)	*S. (S.) schneideri*
6′	Tail longer (2–3 times or more than the anal body diameter in length)	*S. (S.) hopperi*
7	Body setae long in cervical region only, body length 2–3 mm. Proximal end of spicules hook-like in shape	*S. (S.) laevis*
7′	Body setae long throughout the length of the body, body length less than 1·6 mm	8
8	Amphids greater than 50% of the corresponding head diameter	*S. (S.) gerlachi*
8′	Amphids less than 50% of the corresponding head diameter	9
9	Sub-cephalic setae present anterior to cephalic setae, cervical setae up to 15 μm in length	*S. (S.) laevioides*
9′	Sub-cephalic setae absent anterior to cephalic setae, cervical setae 20–22 μm in length	*S. (S.) gnaigeri*
10	Pre-anal supplements present in male	*S (P.) flagellata*
10′	Pre-anal supplements absent in male	11
11	Cervical setae fairly long, other body setae lacking, spicules with only a small club-shaped expansion at the proximal end	*S. (P.) striaticaudata*
11′	Cervical setae short	12
12	Proximal end of spicules markedly hook-shaped, body length about 2 mm	*S. (P.) hamata*
12′	Proximal end of spicules with club-shaped manubrium, not hook-like, body-length less than 2 mm	*S. (P.) mokii*

Species studied

Spirinia (Spirinia) parasitifera (Bastian, 1865)
(Figs 1a; 2a–f; 3a; 5a–c; 8a–b)

Spira parasitifera Bastian 1865; *Spirina parasitifera*: Filipjev, 1918. For full synonymy see Gerlach & Riemann, 1973.

TYPE LOCALITY. Falmouth, Cornwall, England.

MATERIAL STUDIED. 4♂♂ 1♀ from *Laminaria* holdfasts off the west coast of Scotland, near Gallanchmore Farm, situated on the mainland side of the sound of Kerrera, two miles south of Oban, BM(NH) 1961.105–134; 1♂ from sand-flats, Whitstable, Kent BM(NH) 1964.255; 4♂♂, 6♀♀ and 1 juvenile from sand around the roots of *Zostera*, Hannafore, Looe, Cornwall BM(NH) 1985.1.26–29; 9♂♂, 6♀♀ and 4 juveniles from Bras d'Or Lake, Nova Scotia, Canada (12 m coarse bottom) BM(NH) 1985.2.52–54; 1♂ from sediment on the south side of Pigeon Key, Florida, USA BM(NH) 1986. 12–5; 16♂♂, 10♀♀ from *Thalassia* bed, Biscayne Bay, Florida, BM(NH) 1985.2.33,

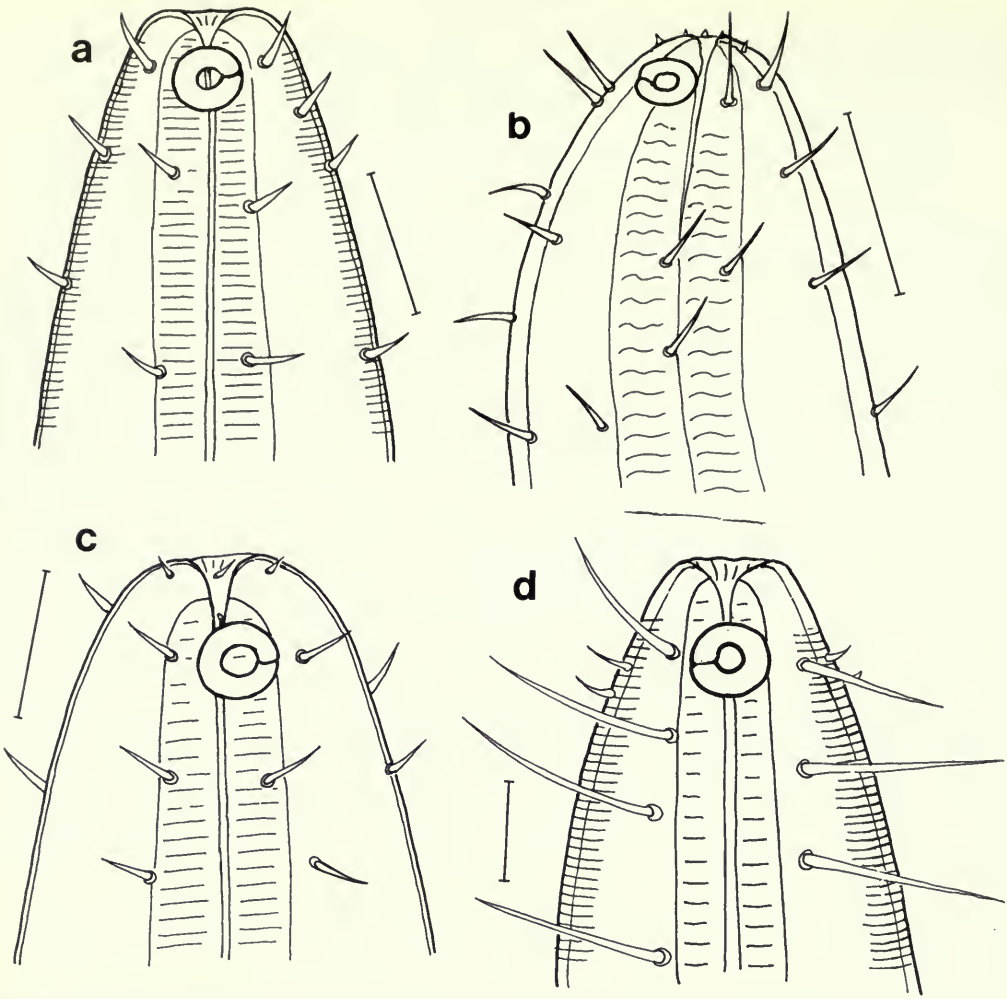

Fig. 1 Lateral views of head of (a) *Spirinia (S.) parasitifera*; (b) *S. (S.) schneideri*; (c) *S. (S.) hopperi*; (d) *S. (S.) laevis*. Bar scales: (a) = 12 μm; (b) = 20 μm; (c) = 10 μm; (d) = 10 μm.

38–40, 43–46; 1♀ from *Diplanthera* bed, Biscayne Bay off Virginia Key, Florida BM(NH) 1985.2.34; 4♂♂, 1♀ from the same locality but from a public beach area BM(NH) 1985.2.35–37, 39; 7♂♂, 3♀♀ from south shore of Pigeon Key, Florida BM(NH) 1985.2.41–42; 3♂♂, 2♀♀ from Quisett Harbour, near Woods Hole, Massachusetts, USA BM(NH) 1985.2.47; 1♂ from Penzance Marsh, Woods Hole, Massachusetts BM(NH) 1985.2.48; 4♂♂, 3♀♀ from Port Monmouth, New Jersey, USA BM(NH)1985.2.49; 10♂♂, 2 juveniles from West Laurencetown, Nova Scotia, Canada BM(NH) 1985.2.50–51.

MEASUREMENTS. Tables I–IV.

SYSTEMATIC NOTES. The specimens examined in the present report agree well with the previous descriptions of this species in most respects. See Stekhoven (1935), Bresslau & Stekhoven (1940) and Warwick (1968). Six labial papillae and a ring of six cephalic papillae, further posteriorly, not always seen or reported before, have been seen with the aid of the scanning electron microscope (see Fig. 8a–b). The four cephalic setae are about 5–6 μm long, situated sublaterally in the region of the anterior end of the amphids.

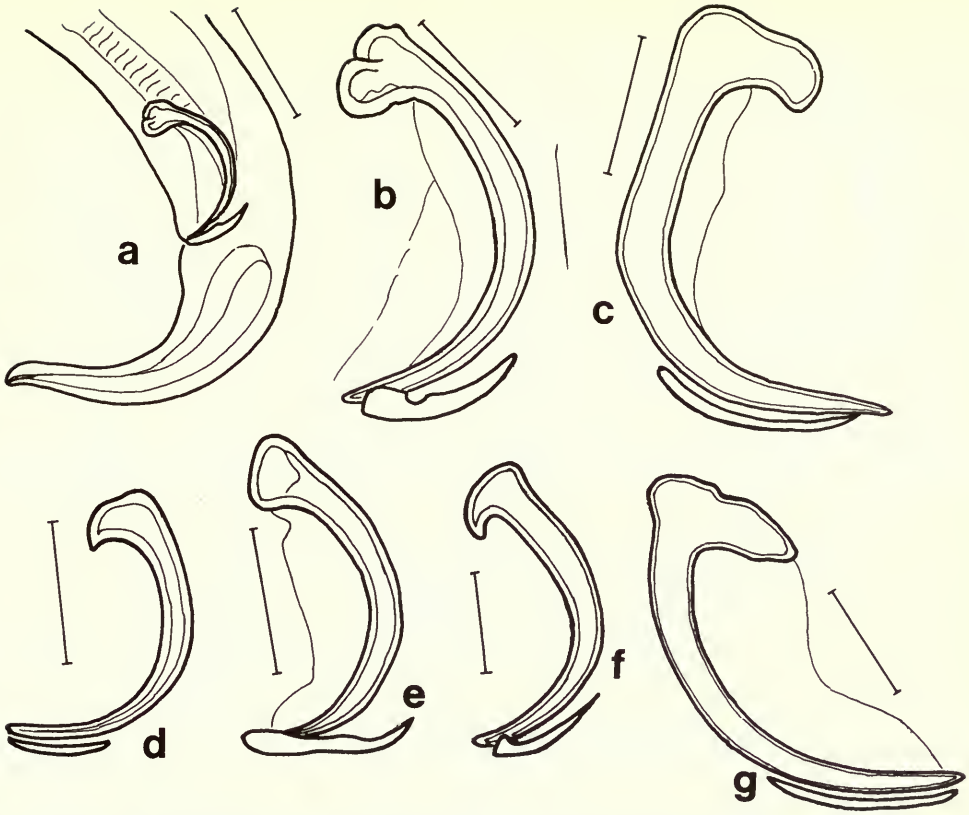

Fig. 2 *Spirinia (S.) parasitifera*: (a) Tail region of male; (b) Lateral view of spicule; (c–f) Variations of spicules in specimens from North America. *S. (Perspiria) hamata* (g) Lateral view of spicule. Bar scales: (a) = 50 μm; (b) = 25 μm; (c) = 15 μm; (d) = 15 μm; (e) = 26 μm; (f) = 15 μm; (g) = 15 μm.

In the specimens examined from British coasts, as well as those from Bras d'Or Lake, Nova Scotia, Canada, the proximal end of the spicules (manubrium) is typically club-shaped (see Fig. 2a–b). The manubrium in the specimens from the other localities in North America, however, is more angular in shape, with variations (see Figs 2c–g, 3a). As this character appears to be the only way in which they differ from the typical form, the North American specimens cannot be considered as representing a different species. It is noted that most of the specimens from Florida are shorter in body-length, but this feature is often known to be the case with the same species found in warmer waters.

Suctoria attached to *S. parasitifera* have been seen in the specimens from Bras d'Or Lake, Nova Scotia, in the same way as Allgén (1934, 1951) found them on *S. parasitifera* from European waters.

GEOGRAPHICAL DISTRIBUTION. Cosmopolitan (see Gerlach & Riemann, 1973 for references prior to that date). It has since been reported from: Strangford Lough, Northern Ireland (Platt, 1977); Ems Estuary, W. Germany (Bouwman, 1981); Island of Sylt, North Sea (Blome, 1982); Loch Etive, Argyllshire, Scotland (Warwick & Gage, 1975); Gallanachmore, Argyllshire (present report); Isles of Scilly (Warwick & Coles, 1977); Exe Estuary, S. Devon, England (Warwick, 1968); Looe, Cornwall; Whitstable, Kent, England (present report); Long Island, Atlantic coast of North America (Tietjen, 1977); Bras d'Or Lake, and West Laurencetown, Nova Scotia, Canada (present report); Florida Keys, Florida; Woods Hole, Massachusetts and Port Monmouth, New Jersey, USA (present report). The record of Cobb (1928), stated as 'locality unknown' in Gerlach & Riemann (1973), was from Woods Hole, Massachusetts, USA.

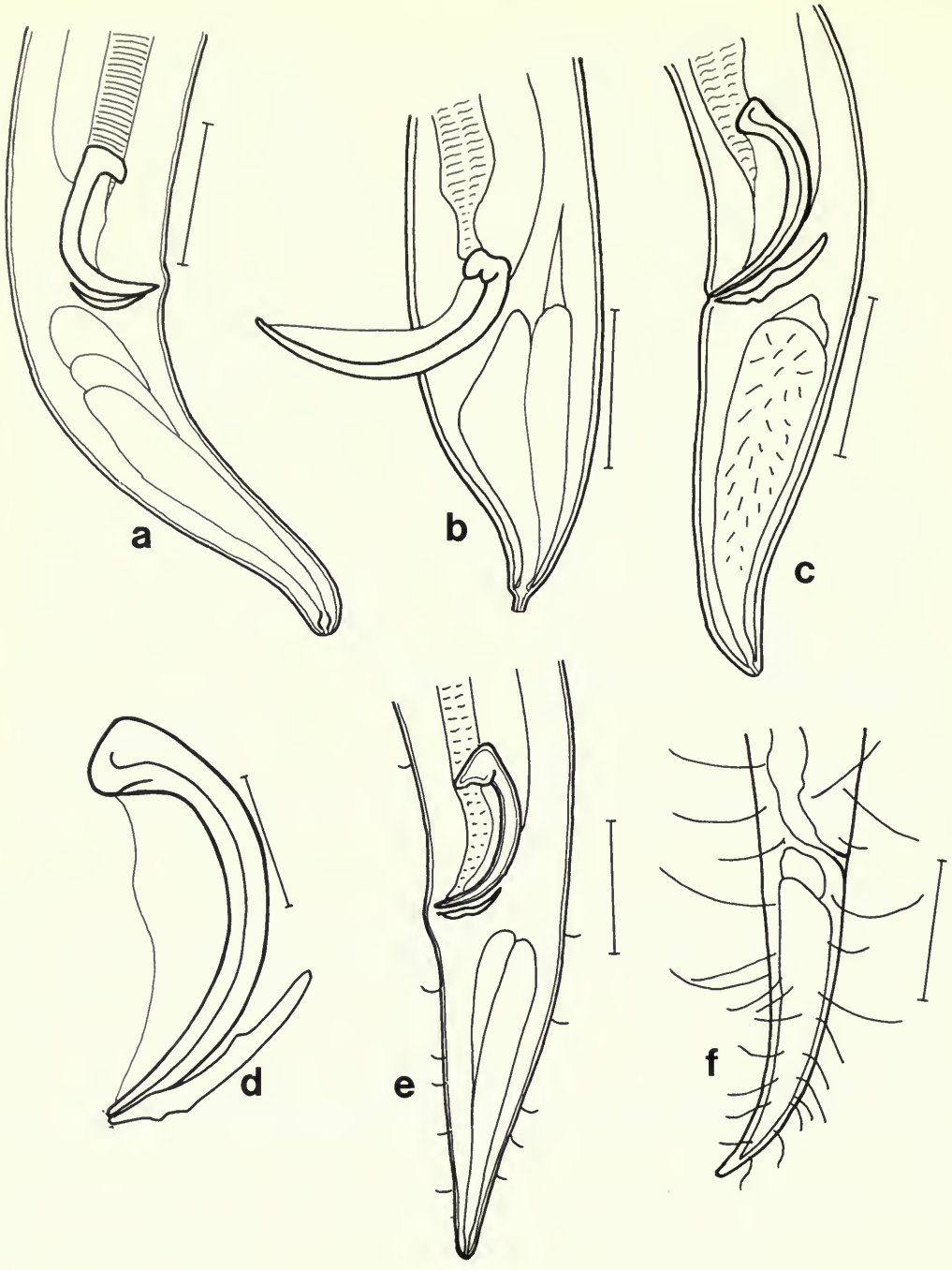

Fig. 3 *Spirinia (S.) parasitifera*:(a) Tail region of male in specimen from Florida. *S. (S.) schneideri* (b) Tail region of male with spicule extended from body, gubernaculum not shown. *S. (S.) hopperi*; (c) Tail region of male; (d) Lateral view of spicule and gubernaculum. *S. (S.) laevis*; (e) Tail region of male. *S. (S.) gerlachi* (f) Tail region of female. Bar scales: (a) = 45 μm; (b) = 75 μm; (c) = 60 μm; (d) = 25 μm; (e) = 50 μm; (f) = 45 μm.

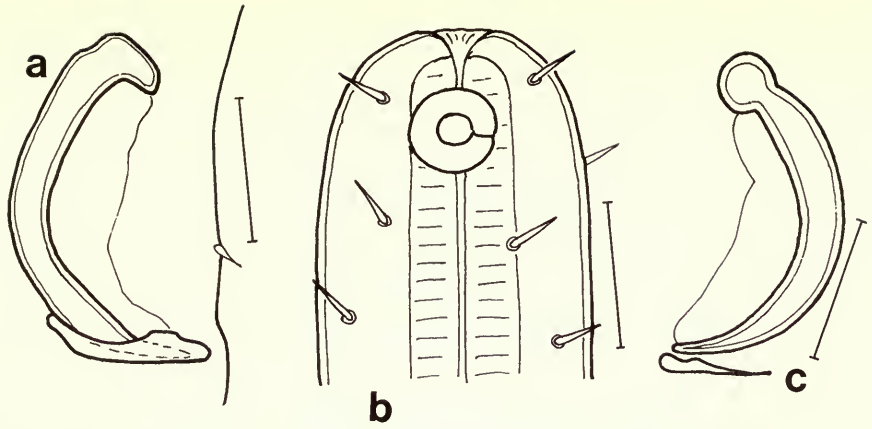

Fig. 4 *Spirinia (Perspiria) mokii*: (a) Lateral view of spicule and gubernaculum; (b) Lateral view of head; (c) Spicule and gubernaculum in holotype specimen. Bar scales: (a) = 20 μm; (b) = 8 μm; (c) = 20 μm.

Spirinia (Spirinia) schneideri (Villot, 1875)
(Figs 1b, 3b, 7a, 9a)

Spira schneideri Villot, 1875. *Spirina schneideri:* Filipjev, 1918.

TYPE LOCALITY. Roscoff, North coast of France.

MATERIAL STUDIED. 4♂♂, 4♀♀ from *Laminaria* holdfasts, Hannafore, Looe, Cornwall, England, BM(NH) 1985.1.30–32; 2♂♂, 2♀♀ in sand, Isles of Scilly, BM(NH) 1980.3.1.

MEASUREMENTS. Table V.

SYSTEMATIC NOTES. This is a large species without cuticular striations. The cephalic sense organs are typical in arrangement (Fig. 9a). The specimens in the present report agree well with the description by Luc & De Coninck (1959). An important distinguishing characteristic is that the tail in both sexes is short, particularly so in the male (see Figs 3b & 7a).

GEOGRAPHICAL DISTRIBUTION. Roscoff, North Coast of Brittany (Villot, 1875); Luc & De Coninck (1959); Atlantic coast of Ireland (Southern, 1914); Looe, Cornwall, England (present report); Isles of Scilly (Warwick & Coles, 1977 and present report).

Spirinia (Spirinia) hopperi sp. nov.
(Figs 1c, 3c–d, 6d–e, 7b, 9b)

TYPE LOCALITY. Wembury Bay, South Devon, England.

MATERIAL STUDIED. 6♂♂, 6♀♀ from a fairly deep rock-pool, approximately MLWS, Wembury Bay, South Devon. Holotype ♂ BM(NH) 1985.1.14; paratypes BM(NH) 1985.1.15–25.

MEASUREMENTS. Table VI.

DESCRIPTION. Cuticle without striations. Lateral fields are prominent, just a little wider than a third of the corresponding body diameter. Six labial papillae have only been seen with the aid of the scanning electron microscope (see Fig. 9b). The intermediate circle of six cephalic sense organs are setose (3–4 μm). The four cephalic setae are about 7–8 μm long situated sublaterally in the region of the centre part of the amphids. The amphids are approximately a third of the corresponding head diameter in width and typical of the genus in shape. Cervical setae are present 8 μm in length. They tend to be arranged in eight longitudinal rows, although rather sporadic, and become sparse towards the region of the posterior end of the oesophagus. Very short setae occur in the anal and tail regions. A small dorsal tooth is present in the narrow mouth cavity. The oesophagus and

Table I. Measurements (in mm) of *Spirinia (S.) parasitifera* (Bastian)

	Specimens from West coast of Scotland					Specimens from Hannafore, Looe, Cornwall										
	♂1	♂2	♂3	♂4	♀1	♂5	♂6	♂7	♂8	♀2	♀3	♀4	♀5	♀6	♀7	J_1
Body-length	2·56	2·60	2·65	2·75	3·20	2·50	2·75	2·80	3·30	2·47	2·70	2·70	2·82	3·00	3·18	1·95
Max. body-breadth	0·05	0·06	0·06	0·07	0·08	0·06	0·07	0·07	0·07	0·08	0·08	0·10	0·08	0·08	0·10	0·04
Head-diameter	0·015	0·015	0·015	0·016	0·020	0·015	—	0·015	0·017	0·012	0·017	0·013	0·013	0·015	0·016	0·01
Length of oesophagus	0·14	0·15	0·16	0·16	0·19	0·16	0·16	0·15	0·16	0·14	0·16	0·15	0·16	0·15	0·16	0·14
Tail-length	0·15	0·12	0·14	0·14	0·14	0·14	0·14	0·13	0·16	0·14	0·14	0·17	0·18	0·15	0·16	0·13
Distance of nerve-ring from ant. end.	0·09	0·09	0·10	0·10	0·10	0·10	0·10	0·08	0·10	—	0·11	0·10	0·10	0·09	0·10	0·09
Anal-diameter	0·04	0·04	0·04	0·04	0·06	0·04	0·04	0·06	0·06	0·04	0·05	0·05	0·06	0·05	0·05	0·04
Length of spicules	0·08	0·10	0·09	0·08	—	0·09	0·08	0·09	0·10	—	—	—	—	—	—	—
Length of gubernaculum	0·02	0·03	0·03	0·03	—	0·03	0·03	0·03	0·04	—	—	—	—	—	—	—
Distance of vulva from ant. end.	—	—	—	—	—	—	—	—	—	1·15	1·25	1·30	1·32	1·30	1·50	—

Table II. Measurements (in mm) of *Spirinia (S.) parasitifera* (Bastian)

	Specimens from Bras d'Or Lake, Nova Scotia, Canada											
	♂$_9$	♂$_{10}$	♂$_{11}$	♂$_{12}$	♂$_{13}$	♂$_{14}$	♂$_{15}$	♀$_8$	♀$_9$	♀$_{10}$	♀$_{11}$	J_2
Body-length	2·00	2·25	2·40	2·50	2·52	2·55	2·65	2·02	2·50	2·55	2·75	2·05
Max. body-breadth	0·04	0·04	0·05	0·05	0·06	0·04	0·06	0·05	0·06	0·08	0·07	0·05
Head-diameter	0·017	0·017	0·018	0·018	0·017	0·017	0·018	0·017	0·017	0·018	0·018	0·013
Length of oesophagus	0·13	0·15	0·14	0·13	0·15	0·15	0·15	0·14	0·15	0·15	0·15	0·14
Tail-length	0·14	0·13	0·14	0·16	0·15	0·13	0·16	0·10	0·16	0·15	0·17	0·15
Distance of nerve-ring from ant. end.	0·08	0·10	0·09	0·08	0·09	0·09	0·09	0·09	0·10	0·09	0·08	0·09
Anal-diameter	0·04	0·03	0·04	0·04	0·04	0·04	0·04	0·04	0·04	0·04	0·03	0·03
Length of spicules	0·06	0·06	0·06	0·06	0·07	0·07	0·07	—	—	—	—	—
Length of gubernaculum	0·02	0·02	0·02	0·02	0·03	0·02	0·03	—	—	—	—	—
Distance of vulva from ant. end.	—	—	—	—	—	—	—	1·02	1·26	1·25	1·32	—

Table. III. Measurements (in mm) of *Spirinia (S.) parasitifera* (Bastian)

	Specimens from near Woods Hole, Massachusetts, USA				Specimens from West Laurencetown, Nova Scotia, Canada								
	♂16	♂17	♂18	♀12	♂19	♂20	♂21	♂22	♀13	♀14	♀15	♀16	♀17
Body-length	2·52	2·55	2·95	2·47	2·40	2·60	2·70	2·80	2·05	2·10	2·50	2·50	2·60
Max. body-breadth	0·05	0·07	0·07	0·08	0·05	0·05	0·06	0·05	0·07	0·07	0·08	0·06	0·07
Head diameter	0·015	0·012	0·013	0·015	0·017	0·015	0·017	0·015	0·018	0·015	0·016	0·018	0·015
Length of oesophagus	0·15	0·14	0·15	0·15	0·15	0·14	0·16	0·16	0·16	0·15	0·16	0·16	0·15
Tail-length	0·14	0·16	0·15	0·14	0·13	0·14	0·14	0·13	0·14	0·12	0·14	0·12	0·13
Distance of nerve-ring from ant. end.	0·09	0·09	0·08	0·09	0·09	0·08	0·10	0·09	0·09	0·09	0·08	0·09	0·09
Anal-diameter	0·04	0·04	0·04	0·04	0·04	0·04	0·04	0·04	0·04	0·03	0·03	0·04	0·04
Length of spicules	0·07	0·06	0·09	—	0·06	0·07	0·05	0·07	—	—	—	—	—
Length of gubernaculum	0·03	0·02	0·03	—	0·015	0·02	0·015	0·02	—	—	—	—	—
Distance of vulva from ant. end.	—	—	—	1·15	—	—	—	—	0·65	1·10	1·30	1·20	1·20

Table IV. Measurements (in mm) of *Spirinia (S.) parasitifera* (Bastian) from localities in Florida, USA

	♂23	♂24	♂25	♂26	♂27	♂28	♂29	♂30	♀18	♀19	♀20	♀21	♀22	♀23
Body-length	1·65	1·80	1·85	1·90	1·90	1·95	1·95	2·15	1·65	1·70	1·69	1·80	1·90	1·91
Max. body-breadth	0·06	0·06	0·06	0·05	0·05	0·05	0·06	0·05	0·06	0·07	0·06	0·06	0·06	0·06
Head-diameter	0·017	0·017	0·016	0·016	0·016	0·017	0·017	0·017	0·016	0·017	0·017	0·016	0·016	0·016
Length of oesophagus	0·13	0·13	0·13	0·12	0·12	0·13	0·12	0·15	0·11	0·13	0·12	0·11	0·14	0·13
Tail-length	0·10	0·10	0·13	0·12	0·12	0·11	0·10	0·12	0·12	0·10	0·10	0·08	0·11	0·10
Distance of nerve-ring from ant. end.	0·08	0·09	0·06	0·06	0·07	0·08	0·08	0·09	0·06	0·08	0·08	0·07	0·06	0·08
Anal-diameter	0·04	0·04	0·04	0·04	0·03	0·04	0·04	0·04	0·03	0·04	0·03	0·03	0·04	0·03
Length of spicules	0·07	0·06	0·06	0·05	0·07	0·06	0·06	0·07	—	—	—	—	—	—
Length of gubernaculum	0·03	0·02	0·02	0·02	0·03	0·02	0·03	0·03	—	—	—	—	—	—
Distance of vulva from ant. end	—	—	—	—	—	—	—	—	0·77	0·90	0·82	0·85	0·95	0·94

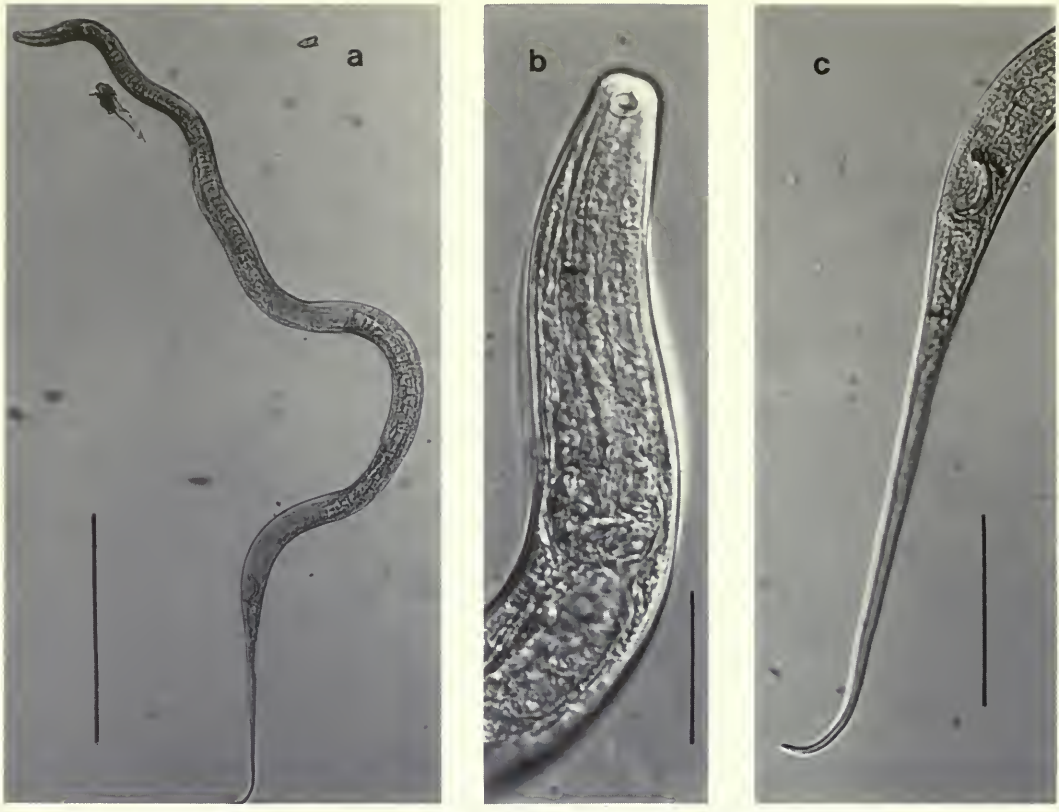

Fig. 5 *Spirinia (S.) parasitifera*: (a) male specimen; (b) oesophageal region; (c) Tail region of male. Bar scales: (a) = 500 μm; (b) = 75 μm; (c) = 50 μm.

Table V. Measurements (in mm) of *Spirinia (S.) schneideri* (Villot)

	Specimens from Hannafore, Looe, Cornwall						Specimens from Isles of Scilly			
	♂1	♂2	♀1	♀2	♀3	♀4	♂3	♂4	♀5	♀6
Body-length	4·40	5·20	4·50	4·55	4·70	4·80	4·75	6·00	4·75	5·70
Max. body-breadth	0·11	0·14	0·13	0·12	0·13	0·13	0·12	0·13	0·15	0·16
Head-diameter	0·015	0·02	0·017	0·017	0·02	0·02	0·02	0·02	0·02	0·02
Length of oesophagus	0·21	0·25	0·21	0·23	0·24	0·24	0·22	0·25	0·25	0·25
Tail-length	0·14	0·16	0·14	0·13	0·14	0·13	0·14	0·14	Tail bent	0·14
Distance of nerve-ring from ant. end	0·13	0·15	0·13	0·12	0·15	0·16	0·14	0·18	0·15	0·16
Anal-diameter	0·10	0·12	0·10	0·09	0·09	0·09	0·09	0·12	—	0·10
Length of spicules	0·13	0·16	—	—	—	—	0·17	0·18	—	—
Length of gubernaculum	0·03	0·05	—	—	—	—	0·17	0·18	—	—
Distance of vulva from ant. end	—	—	2·05	1·95	Not seen	2·10	—	—	2·32	2·40

Table VI. Measurements (in mm) of *Spirinia (S.) hopperi* sp. nov.

	♂1	♂2	♂3	♂4	♂5	♂6	♀1	♀2	♀3	♀4	♀5	♀6
Body-length	4·10	4·50	4·90	4·80	5·10	5·40	4·70	4·80	4·90	4·92	5·10	5·30
Max. body-breadth	0·08	0·08	0·08	0·10	0·10	0·08	0·10	0·10	0·10	0·10	0·10	0·11
Head-diameter	0·02	0·02	0·02	0·02	0·02	0·02	0·02	0·02	0·02	0·02	0·02	0·02
Length of oesophagus	0·20	0·22	0·22	0·23	0·24	0·26	0·22	0·24	0·20	0·21	0·24	0·24
Tail-length	0·18	0·16	0·18	0·20	0·21	0·18	0·17	0·21	0·18	0·20	0·18	0·20
Distance of nerve-ring from ant. end.	0·12	0·12	0·13	0·14	0·15	0·14	0·12	0·13	0·11	0·12	0·14	0·14
Anal-diameter	0·07	0·07	0·08	0·07	0·07	0·08	0·06	0·06	0·06	0·06	0·06	0·06
Length of spicules	0·11	0·12	0·12	0·11	0·12	0·13	—	—	—	—	—	—
Length of gubernaculum	0·04	0·06	0·04	0·05	0·05	0·05	—	—	—	—	—	—
Distance of vulva from ant. end.	—	—	—	—	—	—	1·90	2·10	1·95	1·92	2·20	2·20

intestine are typical of the genus. The oesophageal bulb is 35 μm in width (about 60% of the corresponding body diameter in width) and about 40 μm in length. The tail is conical and fairly long in both sexes (see Figs 3c, 7b).

MALE. The testis is single, anterior and outstretched, commencing near the anterior end of the intestine and running ventro-laterally to the right of it throughout its length. The vas deferens is long and muscular in appearance and terminates with a narrow duct to the cloaca. The spicules are fairly long and quite prominent, with a slight expansion (manubrium) at the proximal end. The gubernaculum consists of two pieces, a little less than half as long as the spicules. A ventral ala (or velum) is present on each spicule (see Fig. 3c–d).

FEMALE. The ovaries are paired and antidromously reflexed, situated laterally to the left of the intestine. Up to eight eggs have been seen at a time, 3 in the anterior uterus and 5 in the posterior uterus. They measure 140 × 70 μm–150 × 80 μm in size. The vulva, as a small transverse slit, is situated ventrally half-way along the length of the body.

DIFFERENTIAL DIAGNOSIS. This species, in common with *S. schneideri,* differs from all other species of *Spirinia* in the absence of cuticular transverse striations. It is about the same length as *S. schneideri* (up to just over 5 mm) but differs from that species in having a fairly long conical tail. The shape of the spicules and gubernaculum are also characteristic.

ETYMOLOGY. I name this species after Mr Bruce E. Hopper, who first suggested that I investigate the species belonging to the genus *Spirinia.*

GEOGRAPHICAL DISTRIBUTION. Wembury Bay, South Devon, England (present report).

Spirinia (Spirinia) laevis (Bastian, 1865)
(Figs 1d, 3e, 6a, 8c)

Spira laevis Bastian, 1865; *Spirina laevis:* Filipjev, 1918; *Spirina pilosa* Allgén, 1935.

TYPE LOCALITY. Falmouth, Cornwall, England.

MATERIAL STUDIED. 3♂♂, 1♀ Exe Estuary, S. Devon (in sand) BM(NH) 1985 1.1–3; 6♂♂, 5♀♀ from Hannafore, Looe, Cornwall (in *Laminaria* holdfasts) BM(NH) 1985.1.4–13.

MEASUREMENTS. Table VII.

SYSTEMATIC NOTES. The specimens examined in the present report conform well with the previous descriptions. The transverse cuticular striations are a little coarser compared with those in *S.*

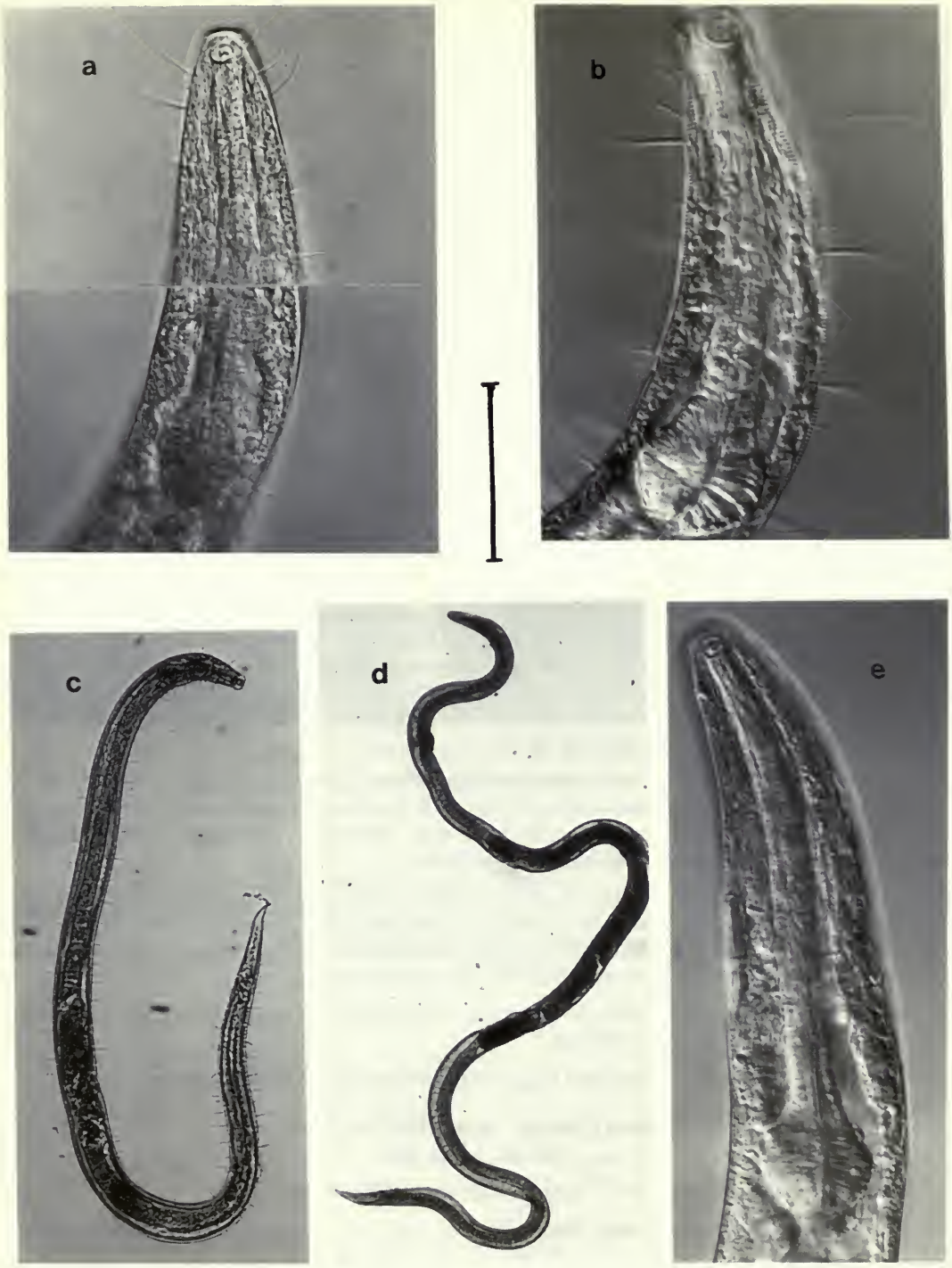

Fig. 6 *Spirinia (S.) laevis* (a) oesophageal region, *Spirinia (S.) gerlachi* (b) oesophageal region; (c) female specimen. *S. (S.) hopperi* (d) female specimen; (e) oesophageal region. Bar scales: (a) = 55 µm; (b) = 40 µm; (c) = 300 µm; (d) = 535 µm; (e) = 60 µm.

Table. VII. Measurements (in mm) of *Spirinia (S.) laevis* (Bastian)

	Specimens from Exe Estuary, Devon				Specimens from Hannafore, Looe, Cornwall								
	♂1	♂2	♂3	♀1	♂4	♂5	♂6	♂7	♂8	♂9	♀2	♀3	♀4
Body-length	3·80	4·12	4·40	3·70	3·62	3·63	3·65	3·65	3·70	3·85	3·02	3·80	4·65
Max. body-breadth	0·06	0·06	0·06	0·06	0·07	0·09	0·08	0·10	0·08	0·07	0·07	0·07	0·08
Head diameter	0·015	0·016	0·020	0·015	0·015	0·017	0·020	0·015	0·020	0·017	0·012	0·012	0·015
Length of oesophagus	0·17	0·16	0·17	0·15	0·17	0·16	0·17	0·17	0·16	0·17	0·15	0·15	0·19
Tail-length	0·15	0·14	0·12	0·10	0·10	0·14	0·13	0·14	0·13	0·13	0·11	0·12	0·15
Distance of nerve-ring from ant. end.	0·10	0·09	0·10	0·09	0·10	0·10	0·11	—	0·11	0·11	0·09	0·10	0·12
Anal-diameter	0·05	0·06	0·06	0·04	0·05	0·08	0·06	0·08	0·06	0·05	0·05	0·05	0·06
Length of spicules	0·07	0·09	0·10	—	0·09	0·08	0·10	0·09	0·08	0·08	—	—	—
Length of gubernaculum	0·02	0·03	0·04	—	0·03	0·02	0·03	0·03	0·03	0·02	—	—	—
Distance of vulva from ant. end.	—	—	—	2·60	—	—	—	—	—	—	1·30	2·28	1·90

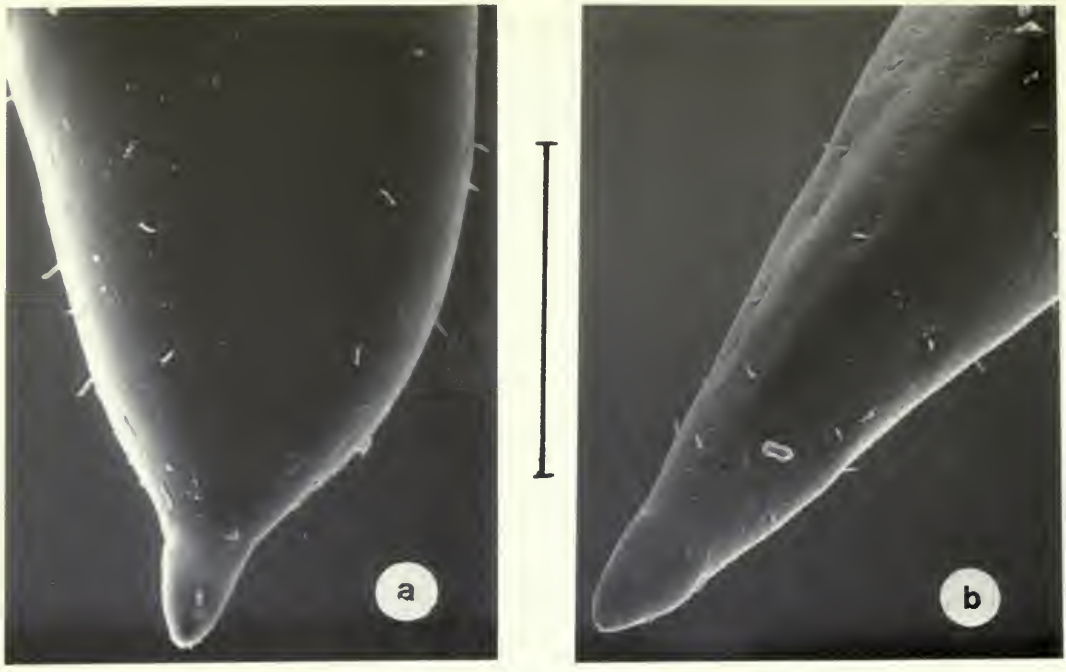

Fig. 7 *Spirinia (S.) schneideri* (a) Tail. *S. (S.) hopperi* (b) Tail. (scanning electron micrographs). Bar scale = 40 μm approx.

parasitifera. An inner crown of six labial papillae, as well as an intermediate ring of six cephalic papillae have been revealed with the aid of the scanning electron microscope. The four cephalic setae measure 20 μm in length. Long cervical setae up to 25 μm in length, as well as shorter subcephalic setae (about 5 μm long) are also present.

S. laevis is known principally from European waters (North Sea and English Channel). It has also been reported from the Atlantic coast of Ireland (Southern, 1914) and the Pacific coast of North America (Wieser, 1959). The description of *S. laevis* from Puget Sound by Wieser (1959) differs from the typical form with regard to the shape of the spicules—the ventral edge being more or less transparent and forming a triangular projection in the middle of the spicule. It seems advisable to wait until more specimens are found off the Pacific coast before regarding this character to be important as distinctive of a different taxon. Wieser (1959) does not state the number of males examined. The ventral edge of the spicule may be a more prominent, or perhaps distorted, ventral ala or velum. The same author also notes differences in the length of the tail, comparing specimens described by Gerlach (1950) as 1·5 anal body diameter long, while Bresslau & Stekhoven (1940) give the tail length as 4 anal body diameters in length. In the Puget Sound specimens the tail measures 3 anal body diameters in length. In the present specimens from the south-west coasts of England, the tail varies from 2 to 3 anal body diameters in length.

GEOGRAPHICAL DISTRIBUTION. See Gerlach & Riemann (1973). It has since been reported from the Island of Sylt, North Sea (Blome, 1982); Exe Estuary, S. Devon and Looe, Cornwall, England (present report).

Spirinia (Spirinia) gerlachi (Luc & De Coninck, 1959)
(Figs 3f, 6b–c)

Spirina gerlachi Luc & De Coninck, 1959

TYPE LOCALITY. Roscoff, Brittany, NW coast of France.

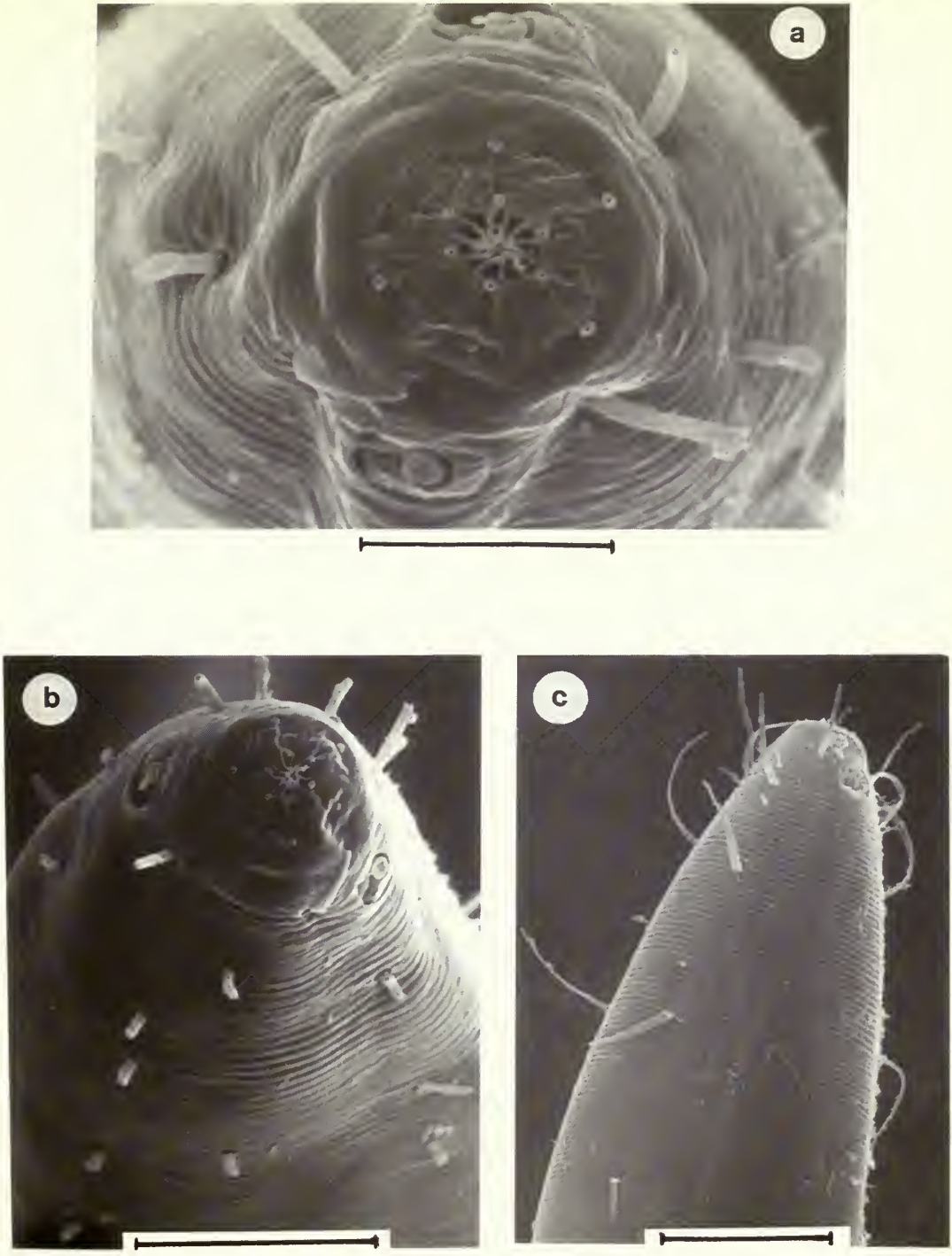

Fig. 8 *Spirinia (S.) parasitifera* (a) apical view of head; (b) anterior end of body. *S. (S.) laevis*: (c) anterior end of body (scanning electron micrographs). Bar scales: (a) = 7 μm; (b) = 15 μm; (c) = 24 μm.

Table VIII. Measurements (in mm) of *Spirinia (S.) gerlachi* (Luc & De Coninck) from Isles of Scilly

	2♂♂	6♀♀	J
Body-length	1·38–1·60	1·40–1·60	1·27
Max. body-length	0·06	0·03–0·06	0·04
Head-diameter	0·02	0·02	0·02
Length of oesophagus	0·12–0·13	0·12–0·13	0·11
Length of tail	0·13	0·11–0·14	0·12
Distance of nerve-ring from ant. end	0·07	0·07–0·08	0·06
Anal-diameter	0·03–0·04	0·03	0·03
Length of spicules	0·03–0·04	—	—
Length of gubernaculum	0·01	—	—
Distance of vulva from ant. end	—	0·68–0·77	—

MATERIAL STUDIED. 2♂♂, 9♀♀, 3 juvenile specimens in sand, Isles of Scilly (Appletree Bay, flats between Tresco and Sampson) BM(NH) 1980.3.2.

MEASUREMENTS. Table VIII.

SYSTEMATIC NOTES. The two male specimens conform to the description given by Luc & De Coninck (1959), except that the somatic setae are longer, measuring up to 50 µm. The testis is situated to the right of the intestine. The females, not described previously, are similar to the males in general body form. Somatic setae in the mid-body region up to 40 µm in length, commencing 30 µm from the anterior end, behind the four cephalic setae which are 10 µm long. They occur in eight longitudinal rows 20–25 µm apart. Short setae present between the rows of long setae and scattered. Amphids 10 µm in diameter. Labial papillae and setae not seen. The ovaries are paired and reflexed, situated laterally to the right of the intestine. Eggs occur in three of the specimens present. In one there is one egg in each uterus and in the other two specimens one egg in the anterior uterus only. They measure 85 µm × 45 µm. Tail in the females similar to that in the males, long and conical with setae nearly to the tip (Fig. 3f).

GEOGRAPHICAL DISTRIBUTION. Roscoff, Brittany, NW coast of France (Luc & De Coninck, 1959); Appletree Bay, Isles of Scilly (Warwick & Coles, 1977 and present report).

Spirinia (Perspiria) hamata Wieser & Hopper, 1967
(Fig. 2g)

TYPE LOCALITY. Florida (Key Biscayne), east coast of North America.

MATERIAL STUDIED. 5♂♂, 2♀♀, 1 juvenile from Avonsport, Nova Scotia, Canada (in Marsh grass) BM(NH) 1985.2.55–56.

MEASUREMENTS. Table IX.

SYSTEMATIC NOTES. The specimens from Nova Scotia examined in the present report conform with the original description by Wieser & Hopper (1967) from Florida, with regard to the males. The proximal end of the spicules (manubrium) is markedly hook-shaped and the spicules are a little longer in the specimens from Nova Scotia. Females, not found previously, agree quite well with the males in general body form, including the long flagellate tail. The ovaries are paired and reflexed. Eggs are present in both of the specimens examined. In one there is one egg in the anterior uterus and one in the posterior uterus. They measure 80 µm × 50 µm and 105 µm × 60 µm respectively. In the other specimen there are two eggs in each uterus. They measure 105 µm × 50 µm–130 µm × 45 µm.

Table IX. Measurements (in mm) of *Spirinia (Perspiria) hamata* Wieser & Hopper from Avonsport, Nova Scotia, Canada

	♂1	♂2	♂3	♂4	♂5	♀1	♀2	J
Body-length	2·05	2·40	2·40	2·40	2·45	2·15	2·40	2·00
Max. body-breadth	0·05	0·05	0·06	0·05	0·05	0·07	0·06	0·05
Head-diameter	0·01	0·015	0·016	0·015	0·015	0·015	0·018	0·011
Length of oesophagus	0·14	0·15	0·13	0·15	0·15	0·13	0·13	0·12
Tail-length	0·36	0·30	0·30	0·30	0·30	0·28	0·32	0·30
Distance of nerve-ring from ant. end	—	—	0·08	0·08	0·08	—	0·09	—
Anal-diameter	0·04	0·04	0·04	0·04	0·35	0·03	0·03	0·03
Length of spicules	0·05	0·07	0·05	0·07	0·06	—	—	—
Length of gubernaculum	0·02	0·03	0·02	0·03	0·02	—	—	—
Distance of vulva from ant. end	—	—	—	—	—	0·92	1·10	—

This species belonging to the subgenus *Perspiria* (type-species) is characterized particularly by the shape of the spicules and gubernaculum—the proximal end of each spicule is markedly hook-shaped.

GEOGRAPHICAL DISTRIBUTION. Florida, east coast of North America (Wieser & Hopper, 1967); Georgia, USA—as *nomen nudum* (Teal & Wieser, 1966); Nova Scotia, Canada (present report).

Spirinia (Perspiria) mokii sp. nov.
(Figs 4a–c, 10a–c)

TYPE LOCALITY. Avicennia Forest, Kuala Selangor, Selangor, Malaysia.

MATERIAL STUDIED. 4♂♂, 2 juveniles from Avicennia and Bruguiera (mangrove) forests, Kuala Selangor, Malaysia. Holotype ♂ BM(NH) 1985.2.57. Paratypes BM(NH) 1985.2.58–62.

MEASUREMENTS. Table X.

DESCRIPTION. The cuticle appears to be smooth throughout most of the body length, but becomes markedly transversely striated on the long and flagellate tail (see Fig 10a–c). The head is truncate and the amphids are situated about 5–7 μm from the anterior end. They are 5 μm in diameter or 40% of the corresponding head diameter in size. Labial papillae have not been seen. The four cephalic setae, which are about 4–5 μm long are situated sublaterally near the anterior margin of the amphids or sometimes a little further back. Cervical setae are also present, of about the same length as the cephalic setae or a little shorter, but scattered. Rugae appear to be present around the stoma but very faint and difficult to see. The buccal cavity is only very slightly cuticularized. No teeth can be made out. The oesophagus is quite short in comparison with the total length of the worm. The oesophageal bulb is quite large in comparison with the corresponding body width (28 μm in width or about 90% of the corresponding body diameter). The tail is very long and filliform with coarse transverse cuticular striations in both sexes.

MALE. The testis is single and straight, situated to the right of the intestine. The spicules are arcuate with a rounded or club-shaped expansion (manubrium) at the proximal end. There is some variation in this respect (see Fig. 4a–c). A velum is present on each spicule. The gubernaculum is short. A single seta is situated mid-ventrally at about half-way between the proximal end of the spicules and the anus.

FEMALE. Not found.

DIFFERENTIAL DIAGNOSIS. This species differs from others belonging to the subgenus *Perspiria* by the shape of the spicules and gubernaculum, the more truncate head and in its small size.

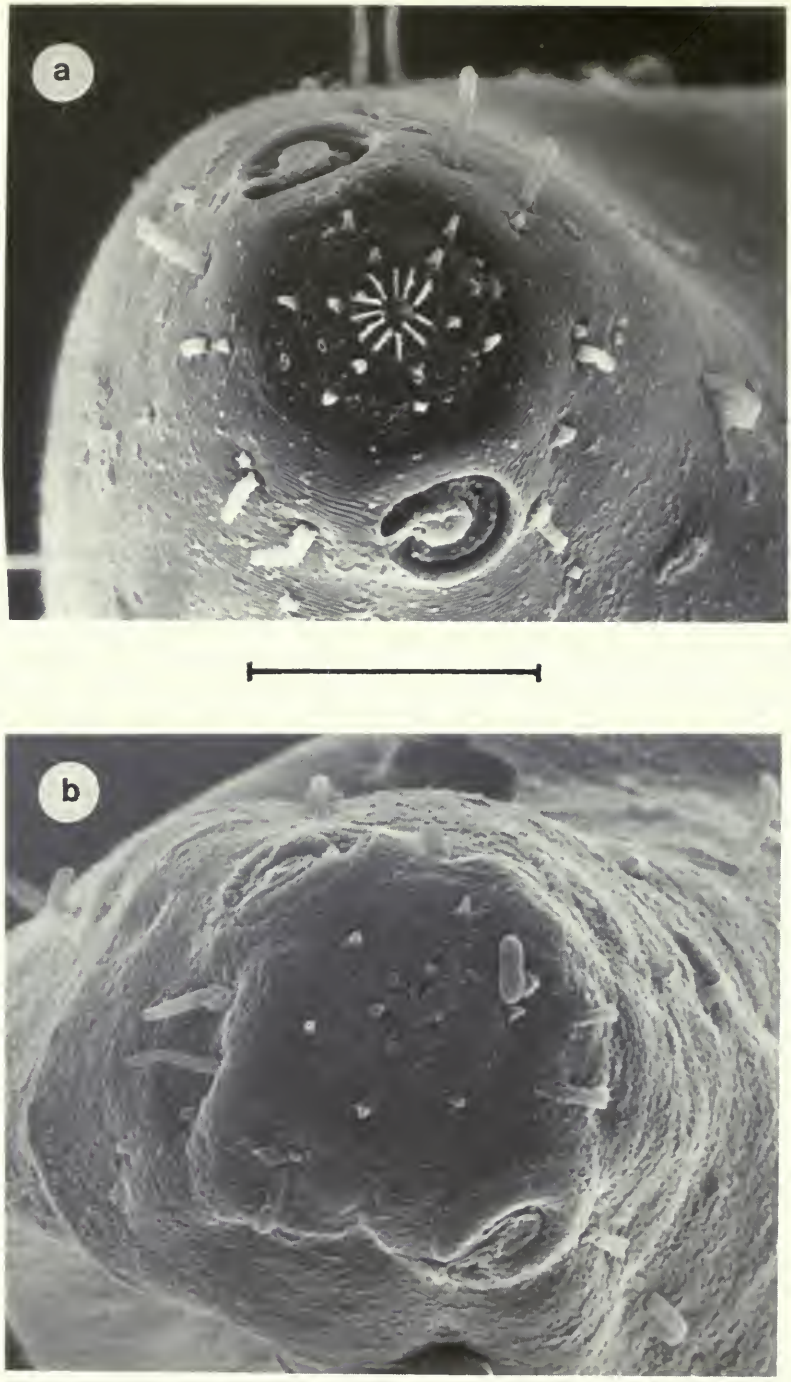

Fig. 9. *Spirinia (S.) schneideri*: (a) apical view of head. *S. (S.) hopperi* (b) apical view of head (scanning electron micrographs). Bar scale = 15 μm.

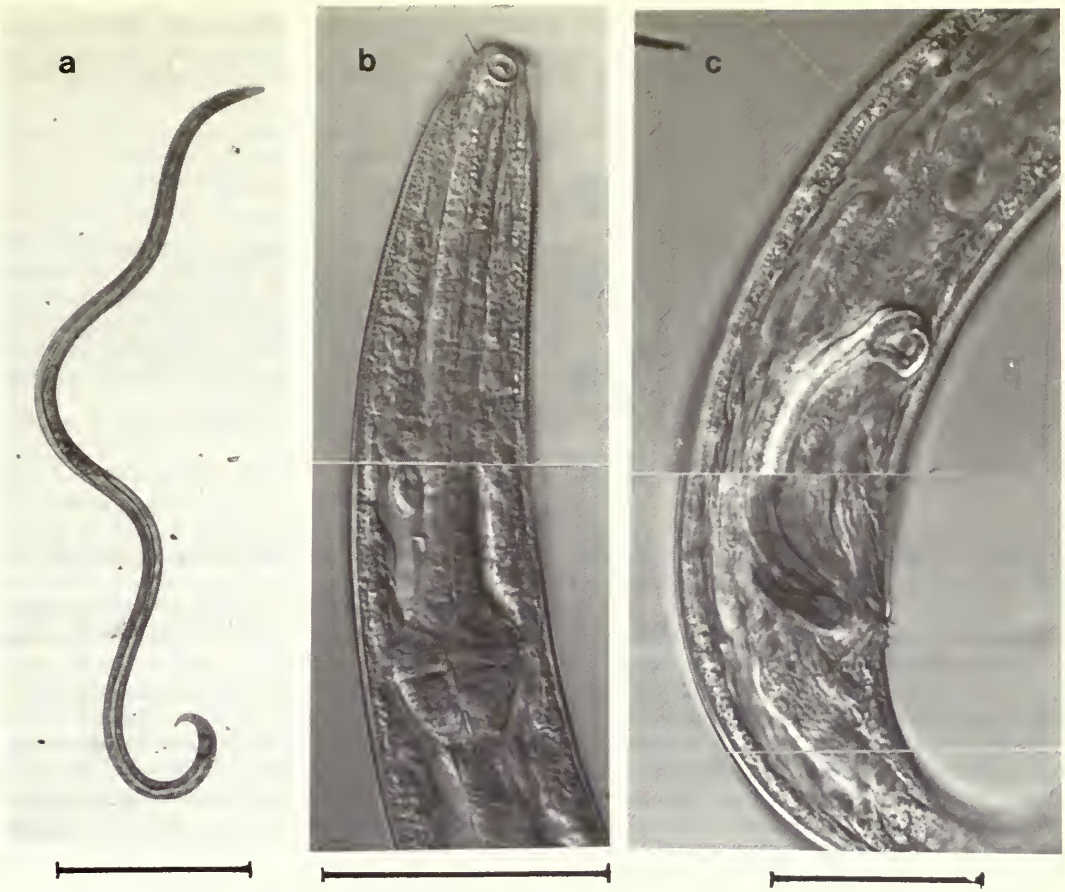

Fig. 10 *Spirinia (Perspiria) mokii*: (a) male specimen; (b) oesophageal region; (c) tail region of male. Bar scales: (a) = 300 μm; (b) = 32 μm; (c) = 100 μm.

Table X. Measurements (in mm) of *Spirinia (Perspiria) mokii* sp. nov. from mangrove forests, Kuala Selangor, Malaysia

	♂1	♂2	♂3	♂4	J1	J2
Body-length	1·60	1·67	1·67	1·69	1·55	1·56
Max. body-breadth	0·05	0·05	0·05	0·04	0·05	0·06
Head-diameter	0·013	0·012	0·013	0·013	0·012	0·013
Length of oesophagus	0·10	0·12	0·12	0·11	0·11	0·11
Tail-length	0·30	0·27	0·31	0·30	0·30	0·27
Distance of nerve-ring from ant. end	0·06	0·07	0·05	0·05	0·07	0·07
Anal-diameter	0·03	0·03	0·03	0·03	0·03	0·03
Length of spicules	0·05	0·04	0·05	0·05	—	—
Length of gubernaculum	0·012	0·01	0·01	0·02	—	—

ETYMOLOGY. The name *mokii* is derived from a North American (Canadian) boys' name.

GEOGRAPHICAL DISTRIBUTION. Avicennia and Bruguira (mangrove) forests, Kuala Selangor, Malaysia (present report).

Acknowledgements

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Caleupodes, a new genus of eupodoid mite (Acari: Acariformes) showing primary opisthosomal segmentation

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Introduction

While sorting a large collection of eupodoid mites, several specimens were found which, although could be assigned to the family Eupodidae, could not be accommodated in any of the existing genera. These specimens are, therefore, considered to represent a new genus and the new taxon *Caleupodes reticulatus* will be described below.

Hitherto, it has been difficult to determine the association between opisthosomal segments, setae and lyrifissures in the Eupodoidea. *C. reticulatus*, however, is unique amongst the known taxa in possessing a clearly segmented opisthosoma. In this study, the segmental boundaries are used to resolve both the number of opisthosomal segments and the relationships between the segments and their structures (setae and lyrifissures).

Although Strandtmann developed a system of setal nomenclature for the Eupodoidea (see Strandtmann, 1967), the standardized notations devised by Grandjean (1947) are here applied to the opisthosomal structures of *C. reticulatus* and other members of the superfamily. This follows the example of other authors who have successfully applied Grandjean's system to a variety of acariform taxa (Knülle, 1959; van der Hammen, 1969; Lindquist, 1977; Quiros-Gonzalez & Baker, 1984) and, as a consequence, simplified the comparison of homologous opisthosomal segments.

Terminology

In the description of *C. reticulatus*, the notations for opisthosomal segments, their setae and lyrifissures are those of Grandjean (1947). Setae of the genital area are named in accordance with their homologues in other taxa and are based on Grandjean (1949). Terms used in this paper are compared with those proposed by Strandtmann (1967) in Table 1. Notations for other setae will be discussed in a subsequent paper on the Eupodoidea relating nomenclature to ontogeny (Baker, in prep.). In the interim, the system of Strandtmann (1967) is used.

Superfamily **EUPODOIDEA**

A general account of the external morphology of eupodoid mites is given by Strandtmann (1971), while the systematics are outlined in Kethley (1982).

Family **EUPODIDAE**

Genus ***Caleupodes*** gen. n.

DEFINITION. Small (300–330 μm long), soft-bodied mites, clearly divided into propodosoma and opisthosoma; blunt epivertex, not delimited dorsally, obvious as overhanging lobe in lateral view; opisthosoma divided into segments dorsally by transverse furrows of differentiated integument; dorsum of body with 12 pairs setae, three pairs lyrifissures; trichobothria filiform; palp tibiotarsus long, slender, tapering; genital setae in single file; anus ventro-terminal; two pairs pseudanal setae; one pair ventral lyrifissures; all legs shorter than body, slender, with no enlarged segments; rhagidial organs recumbent in pits, not T-shaped.

MALES AND IMMATURES. Unknown.

Bull. Br. Mus. nat. Hist. (Zool.) **53**(2): 103–113 Issued 29 October 1987

Table 1. Comparison of terms used for opisthosomal setae and lyrifissures of eupodid mites

	Strandtmann (1967)	This paper (see Figs 1–3)
Opisthodorsum—setae:	ih	c_1*
	eh	c_2
	d_1	d_2
	d_2	e_1
	il	f_1
	el	f_2
	is	h_1
	es	h_2
—lyrifissures:	—	ia
	—	im
	—	ip
Anal region—setae:	a_3	ps_1
	a_1	ps_3
—lyrifissures:	—	ih
Genital area—setae:	igs	eu^+
	egs	g
	pgs	ag

— no name given
* terms below symbol based on Grandjean (1947)
\+ terms below symbol based on Grandjean (1949)

TYPE SPECIES. *Caleupodes reticulatus* sp. n.

DIAGNOSIS. *Caleupodes,* known only from the type species, can be distinguished from other eupodid genera by the presence of external signs of opisthosomal segmentation.

ETYMOLOGY. The name is derived from the Greek 'calos' meaning beauty.

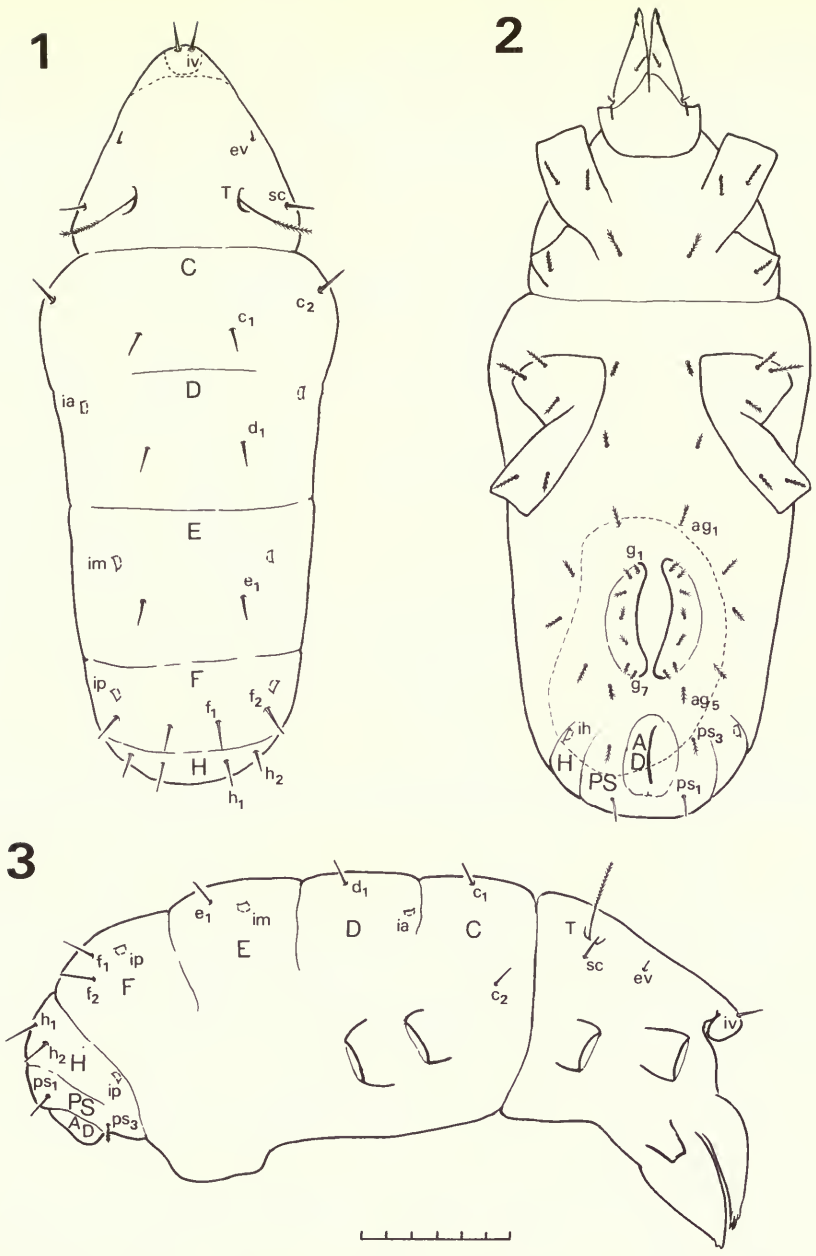
REMARKS. *Caleupodes* is classified in the superfamily Eupodoidea due to the presence of the anterior epivertex and recumbent leg solenidia (rhagidial organs). It is typical of the family Eupodidae in possessing an epivertex without an associated epirostrum, minute apical adoral setae, weakly chelate chelicerae, a tapering palp tibiotarsus, 12 pairs of dorsal setae and lacking adanal setae.

The dimensions, the short setae, the slender femora IV and the genital setae arranged in single file, as seen in *Caleupodes,* agree most closely with the characters of the now invalid genus *Protereunetes* Berlese, whose members are at present included in *Eupodes* C. L. Koch (Fain, 1964; Strandtmann, 1970). *Caleupodes,* however, differs by lacking a distinct epivertex and by possessing two and not three pairs of pseudanal setae.

The species of *Cocceupodes* Thor possess two pairs of pseudanal setae and an epivertex that is not clearly differentiated dorsally. *Caleupodes,* by contrast, lacks the swollen femora IV and the T-shaped rhagidial organs found in *Cocceupodes,* while the internal vertical setae are located on the epivertex and not posterior to it.

Caleupodes reticulatus sp. n.
(Figs 1–14; 19–27; 29–36)

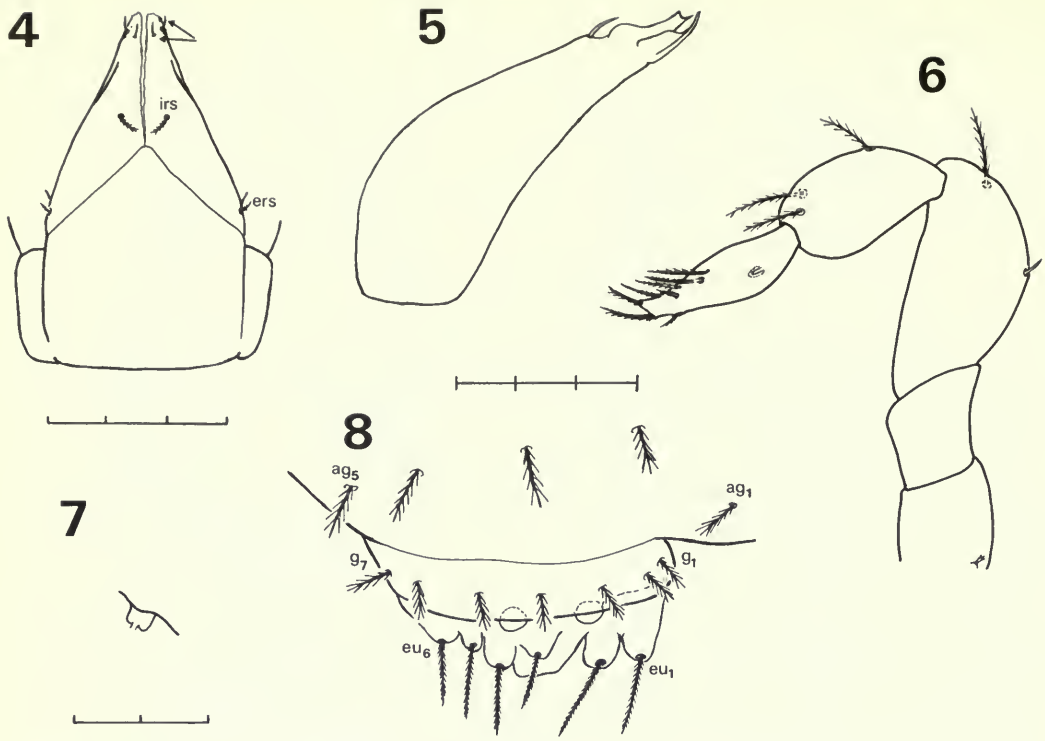
ADULT ♀ (7 specimens examined). With the characters of the genus. Body length 313 μm (300–330), width 152 μm (141–163); distinct sejugal furrow; propodosoma roughly triangular; shoulders of opisthosoma prominent, tapering slightly posteriorly (Figs 1 & 19). *Integument*: conspicuously ornamented, predominantly with reticulations of papillae or spicules linked by fine striae (Figs 20,



Figs 1–3 *Caleupodes reticulatus*: (1) idiosoma, dorsal view; (2) idiosoma and hypostome, ventral view; (3) idiosoma, lateral view. Scale intervals 10 μm.

25–27, 29–31); dorsally, apart from over sejugal furrow and segmental boundaries, some papillae enlarged forming second network (Fig. 20); hypostome, chelicerae, palp tibiotarsus and ventrally surrounding anal and genital shields striate-spiculate.

Dorsum. *Lyrifissures*: *ia, im, ip* located on segments D, E, F respectively (Figs 1 & 3); roughly circular in surface view, laterally appear cup-shaped with pore perforating base (Fig. 7); in SEMs seen as depressed area of smooth cuticle with minute papillae (Fig. 21).

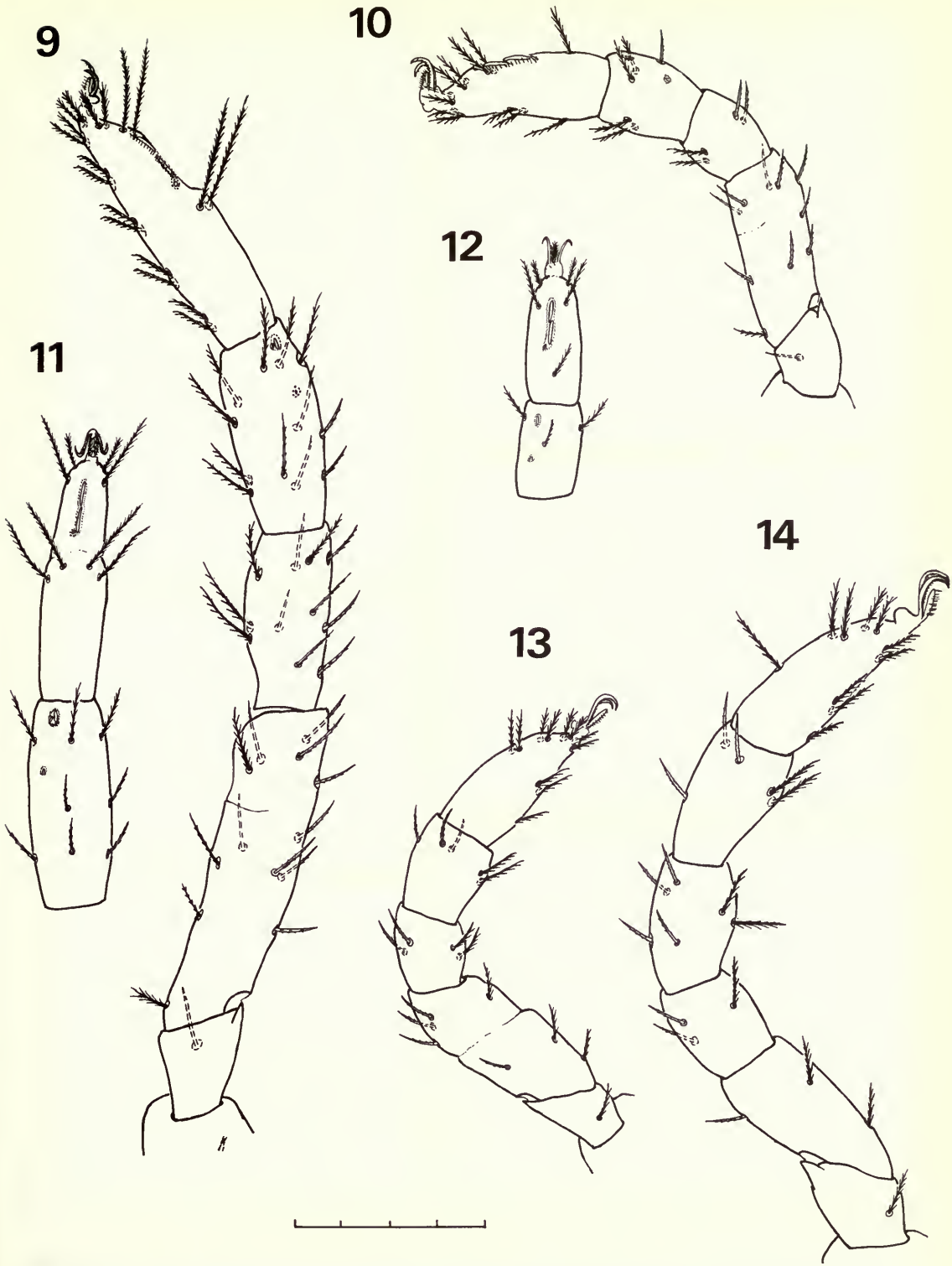


Figs 4–8 *Caleupodes reticulatus*: (4) hypostome, ventral view; (5) chelicera, antiaxial view; (6) palp, antiaxial view; (7) dorsal lyrifissure *im*, lateral view; (8) genital region, lateral view. Scale intervals 10 μm.

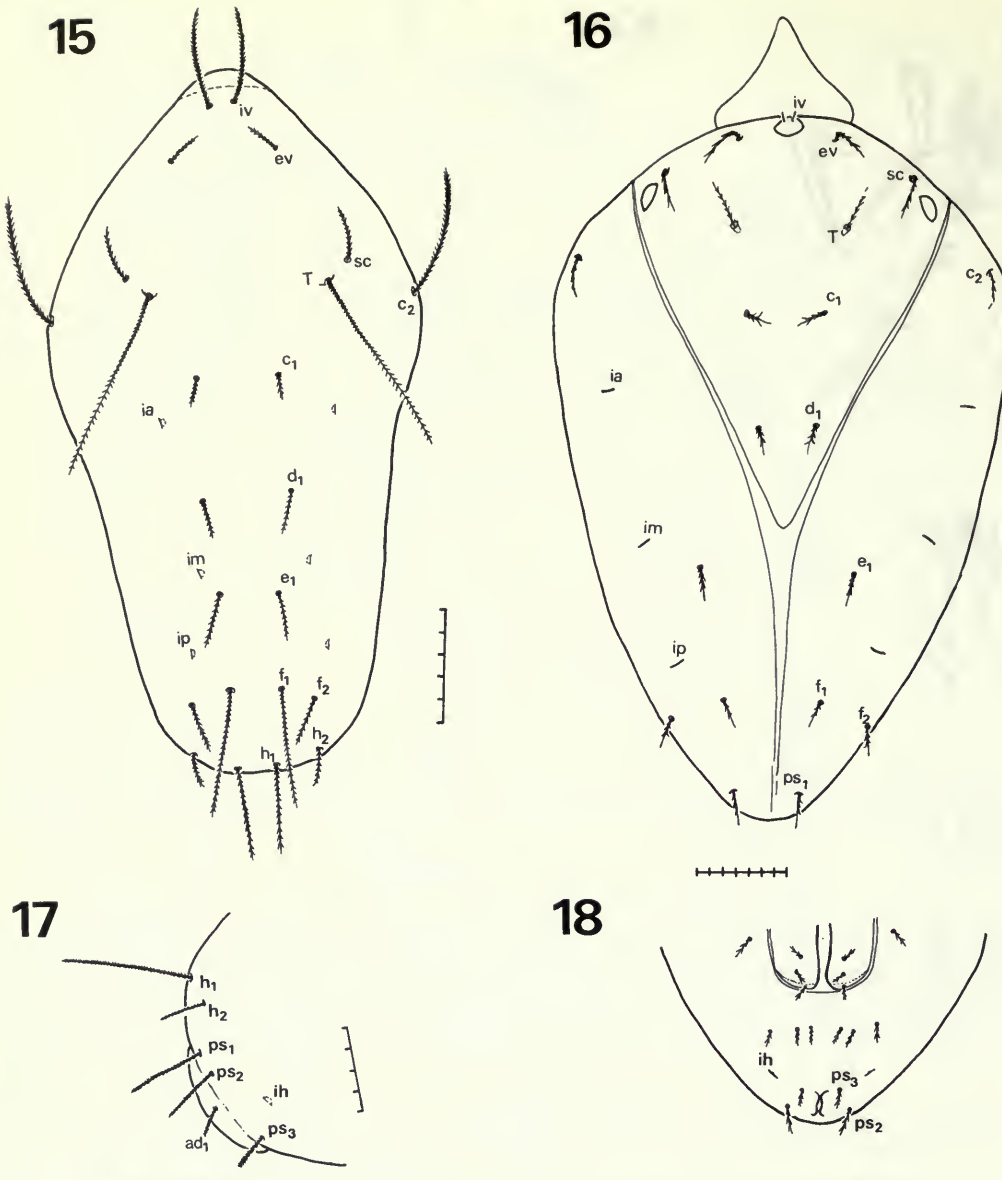
Dorsal setae: arranged as in Fig. 1; trichobothria (*T*) 33 μm (31–35), spinose, markedly so in distal half, inserted in enlarged pit (Fig. 22); other setae fine, taper to point, appear smooth or sometimes weakly serrate under optical microscope, SEMs though show external verticals (*ev*) to be ridged (Fig. 23), the remainder serrate, increasing in degree from internal verticals (*iv*) to *h* setae (Fig. 24); *iv ca.* 14 μm long, scapulars (*sc*) 16 μm, *ev* distinctly shorter than others at *ca.* 8 μm, opisthosomal setae increase gradually in length from *c* row, *ca.* 15 μm, to *h* row, *ca* 18 μm.

VENTER. *Coxae*: faintly defined; setae 3–1–4–3, arranged as in Fig. 2, plumose (Fig. 25), proximal seta of coxae I, III and IV located outside coxal limits, setae increase in length distally on I, III and IV from *ca.* 10 to 15 μm, seta of II *ca.* 13 μm.
Genital area (Figs 2, 8 & 26): six pairs fine, tapering, pilose eugenital setae (eu_{1-6}), located on short protuberances, eu_3 slightly external to others, *ca.* 10 μm long, remainder subequal, 13–15 μm; seven pairs subequal, 6–8 μm, plumose genital setae (g_{1-7}); five subequal, 9–11 μm, plumose aggenital setae (ag_{1-5}); four gravid females, three with a single egg (Fig. 2), one with two, all eggs reniform, *ca.* 120 μm long.
Anal region (Figs 2, 3 & 27): anus opens onto adanal segment; two pairs pseudanal setae, ps_1 dorsal to anus, *ca.* 13 μm long, serrate, ps_3, *ca.* 10 μm, plumose.
Lyrifissures: one pair, *ih*, ventrally on segment H, just inside anterior limit of segment, lateral to ps_3 (Fig. 2); similar form to dorsal lyrifissures (Fig. 29).

GNATHOSOMA. *Hypostome* (Figs 4 & 5): two pairs smooth, apical adoral setae (arrow, Fig. 30) difficult to discern under optical microscope; one pair plumose internal rostral setae (*irs*), *ca.* 8 μm long; one pair sparsely spined external rostral setae (*ers*), *ca.* 4·5 μm long.
Palps (Fig. 6): total length 103 μm (100–108); setae 1–0–2–3–8, supracoxal seta minute, terminates



Figs 9–14 *Caleupodes reticulatus*: (9) leg I, posterolateral view; (10) leg II, posterolateral view; (11) tarsus and tibia I, dorsal view; (12) tarsus and tibia II, dorsal view; (13) leg III, anterolateral view; (14) leg IV, anterolateral view. Scale intervals 10 μm.

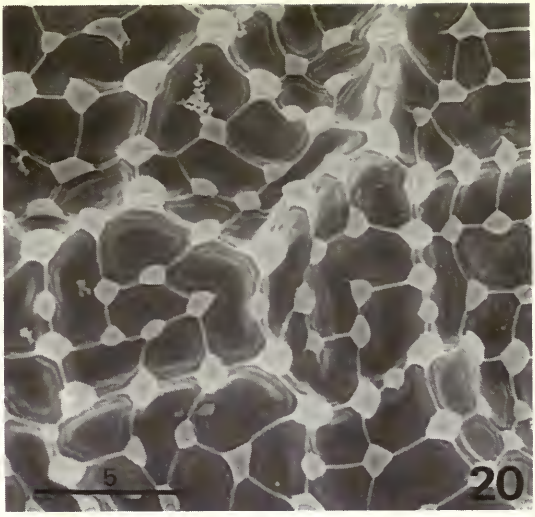


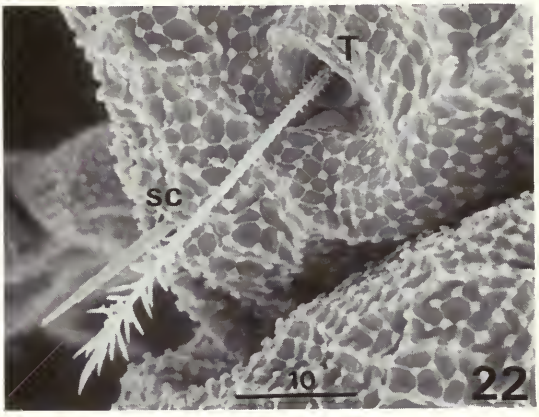
Figs 15 & 16 Idiosoma, dorsal view: (15) *Cocceupodes* sp.; (16) *Penthalodes* sp.

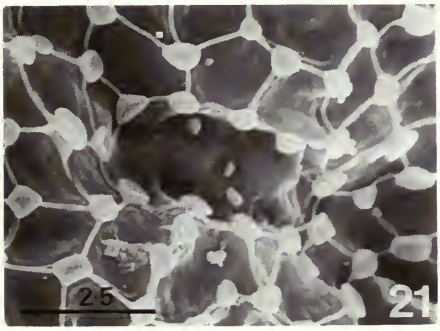
Figs 17 & 18 Anal region: (17) *Rhagidia* sp., lateral view; (18) *Penthalodes* sp., ventral view. Scale intervals 10 μm.

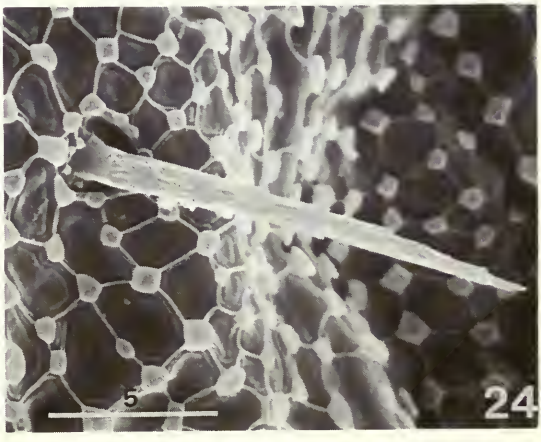
in crown of blunt spicules as in supracoxal seta I (Fig. 32); proximal femoral seta smooth, much shorter than other, spinose femoral seta; tibiotarsal setae inserted marginally and distally, one rhagidiform solenidion located antiaxially.

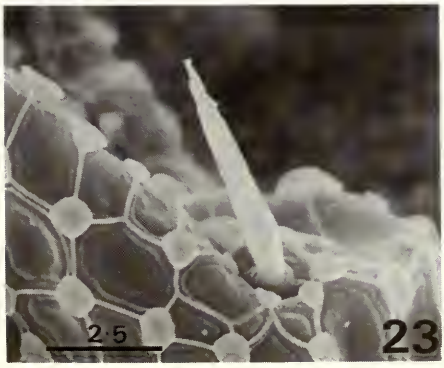
Chelicerae (Fig. 5): total length *ca.* 70 μm; distal end of fixed digit slightly forked; movable digit tapered from distal half; one short, smooth seta inserted on dorsal antiaxial surface just proximal to fixed digit.



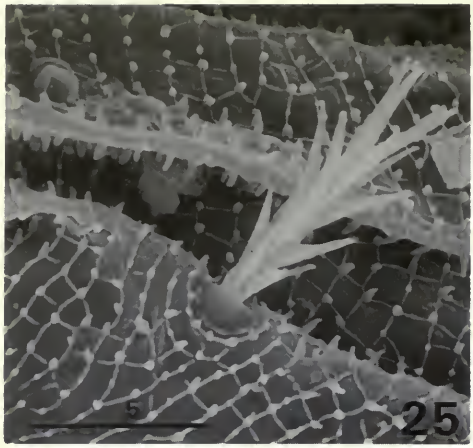


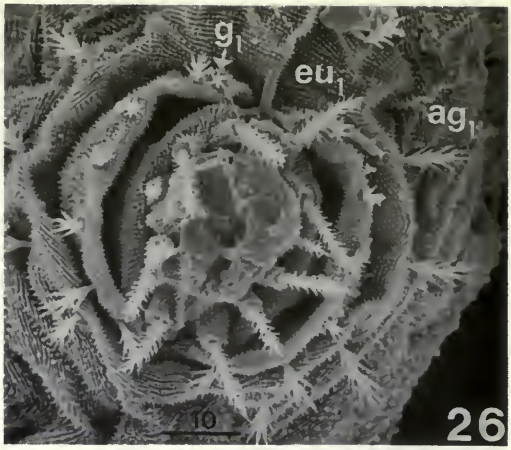


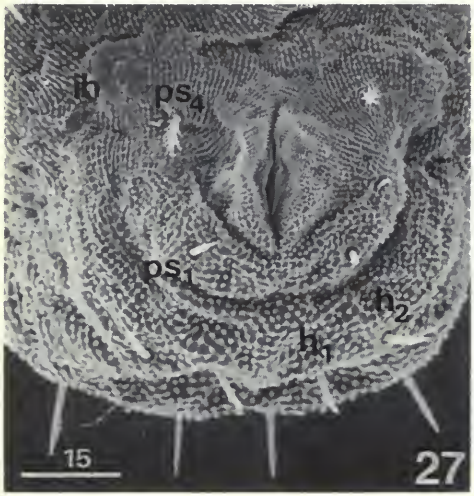


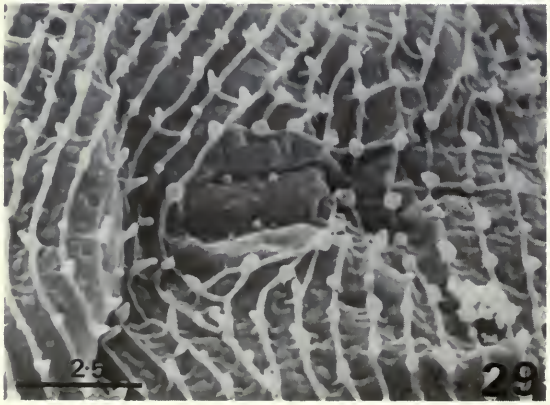


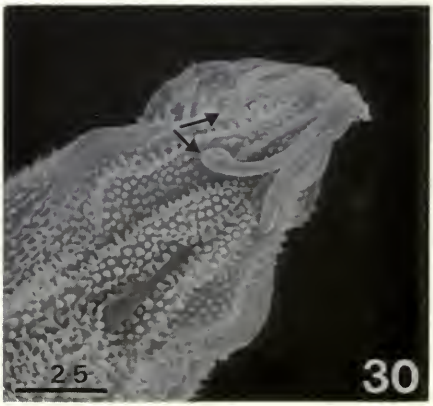
Figs 19–24 *Caleupodes reticulatus*: (19) idiosoma, dorsal view; (20) detail of notogastral integument; (21) dorsal lyrifissure *im*; (22) trichobothrium (T) and scapular seta (sc); (23) external vertical seta; (24) seta h_1. Measurements on scale bars in μm.







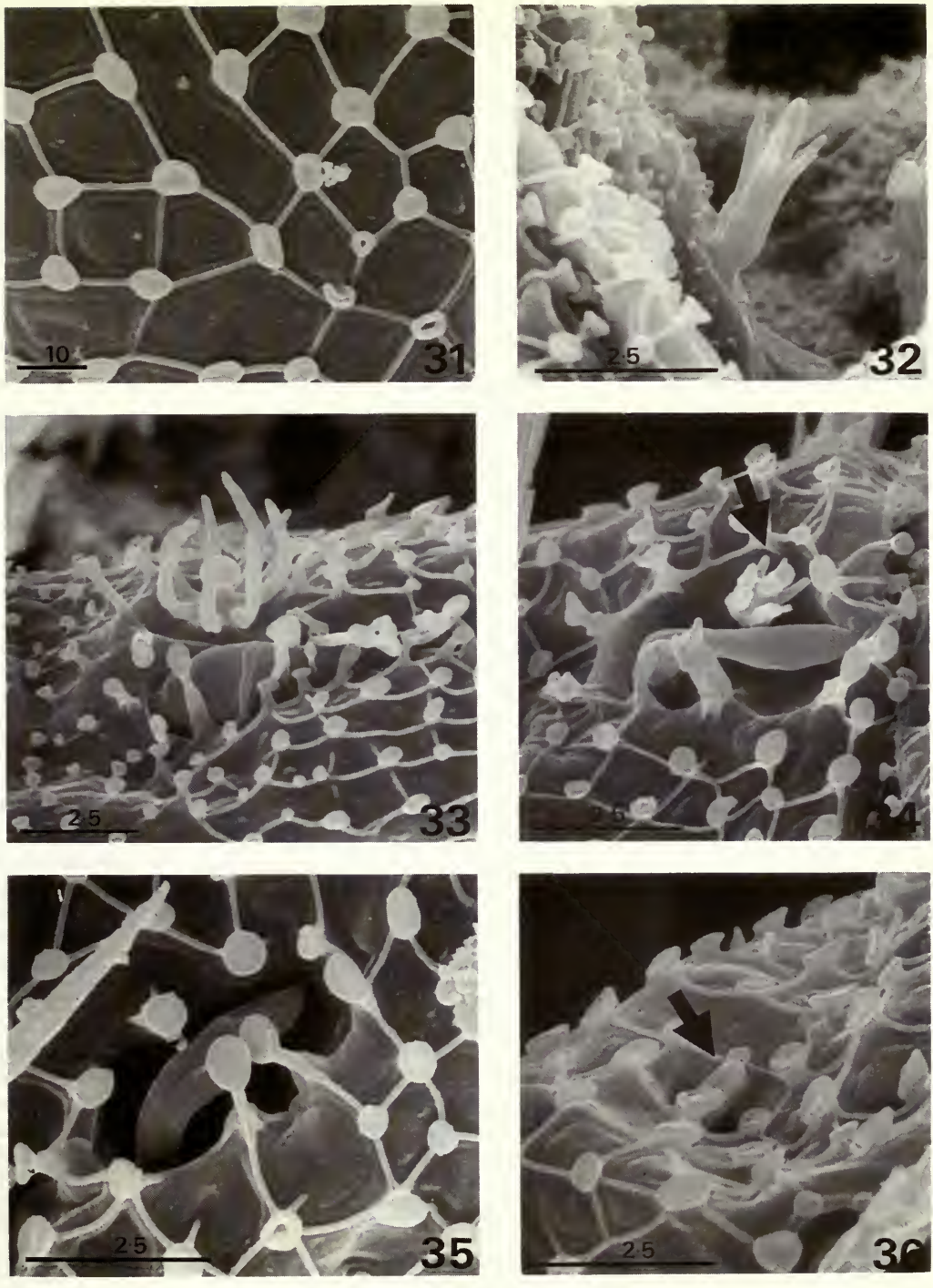




Figs 25–27 *Caleupodes reticulatus*: (25) coxa of leg III, seta and detail of integument; (26) genital region, ventral view; (27) anal region, ventral view.

Fig. 28 *Cocceupodes trisetatus*: anal region of larva, ventral view.

Figs 29 & 30 *Caleupodes reticulatus*: (29) ventral lyrifissure *ih* and detail of integument; (30) apex of hypostome, adoral setae arrowed. Measurements on scale bars in μm.



Figs 31–36 *Caleupodes reticulatus*: (31) femur of leg I, detail of integument; (32) supraxocal seta I; (33) tarsus I, stellate seta; (34) tibia I, distal rhagidial organ, spine with crown of papillae arrowed; (35) tibia II, distal rhagidial organ; (36) tibia I, proximal rhagidial organ, arrowed. Measurements on scale bars in μm.

LEGS (Figs 9–14): first pair approximately three-quarters body length, second and third just below half body length, fourth just above; all femora subdivided, I, II, III faintly; in lateral aspect, tarsus I with dorsal step about halfway along length.
Setae: formulae I 1–13(8+5)–11–12–18, II 1–10(5+5)–4–5–12, III 1–7(3+4)–4–5–11, IV 1–6(3+3)–6–5–10; all moderately short; tarsal setae spinose, on other segments ventral setae spinose, laterals spinose or weakly serrate, dorsals weakly serrate; supracoxal seta I minute, terminates in crown of blunt spicules (Fig. 32).
Rhagidial organs: located as shown in Figs 9–12; those of tarsus I with stellate seta (Fig. 33) adjacent to posterolateral margin of pit at base of proximal organ; those of II subtended by a short, slightly postero-lateral spine within pit; proximal rhagidial organs of tibiae minute (arrow, Fig. 36), distal ones longer (Figs 34 & 35), those of I with associated spine with crown of papillae posterolaterally in pit (arrow, Fig. 34).

MALES AND IMMATURES. Unknown.

DISTRIBUTION. England.

MATERIAL EXAMINED. Holotype ♀, ENGLAND, Suffolk, Hollesley Common, from rotten pine stump, 7.iii.1964 (P. N. & K. Lawrence) (BMNH, reg. no. 1985.7.2.1). Paratypes 6♀♀, same data as holotype (BMNH, reg. nos 1985.7.2.2–7).

Discussion

The furrows of differentiated opisthosomal integument of *C. reticulatus* are considered to indicate boundaries of primary segments. All segments have, at most, one transverse row of setae plus one pair of lyrifissures. These observations parallel those of authors studying other taxa of acariform mites (Grandjean, 1935; Knülle, 1959; Coineau, 1974; Lindquist, 1977). In *C. reticulatus,* seven opisthosomal segments are delimited. Applying Grandjean's (1947) notation system, they are from anterior to posterior, C, D, E, F, H, PS and AD (see Figs 1–3). The segmental boundaries show that lyrifissures *ia, im* and *ip* are located on segments D, E and F respectively, while *ih* is situated ventrally on segment H. D and E both possess a single pair of setae; C, F, H and PS all carry two pairs. The anus opens onto AD, the adanal segment, which is devoid of setae and lyrifissures. The most posterior setae are therefore the pseudanals. Within the Eupodoidea, the maximum number of three pairs of pseudanal setae occurs. The two pairs present in *C. reticulatus* appear to correspond to the most dorsal and ventral of these and so are respectively denoted ps_1 and ps_3. Setae ps_1 are of the same form as those which occur on the dorsum of the body, whereas ps_3 are like those found ventrally, illustrating the 'caudal bend' as discussed by Sitnikova (1978).

Larval acariform mites possess six opisthosomal segments (Grandjean, 1954), or five segments and a telson (Anderson, 1973; Aeschlimann & Hess, 1984), consequently the seven present in *C. reticulatus* indicate that one is added after the larval stage. Unfortunately, attempts to collect immature stages of *C. reticulatus* have been unsuccessful and so it has not been possible to study the ontogenetic development. Furthermore, the lack of postlarval addition of opisthosomal setae and lyrifissures in eupodid and penthalodid mites provides no evidence for anamorphosis (Pittard, 1971; Gless, 1972). Observations of larvae of other eupodid species, however, suggest that a segment is indeed added subsequently. The anal shields in the larva of *Cocceupodes trisetatus* Strandtmann & Prasse bear two pairs of setae while the ventral lyrifissures, *ih,* lie close to the junction of the shields and the surrounding integument (Fig. 28). In the adult *C. reticulatus,* by contrast, the anal shields are devoid of setae while *ih* are located some way from the anus (Fig. 27). More support was gained when, contrary to the situation described by other authors (Zacharda, 1980; Kethley, 1982), postlarval setal addition was observed in the Rhagidiidae. As in the other holotrichous eupodoid families, the pseudanal setae (three pairs) are located on the anal flaps of the larva. In the protonymph, however, the pseudanals have moved away from the anus, but the shields now bear a single pair of setae, which are here identified as adanals (ad_1) (Fig. 17).

Apart from the markedly hypertrichous genera of the families Penthaleidae and Strandtmanniidae, the homologues of opisthosomal structures of *Caleupodes* can be identified in the other

eupodoid genera (Figs 15–18). Eight pairs of dorsal setae are normally present, the exception being in the genus *Penthalodes* Murray. Strandtmann (1971) suggests that members of this genus have only six pairs of dorsal setae, the missing ones being d_1 and f_2, and three pairs of pseudanal setae. However, the interpretation of the relationships between opisthosomal segments, setae and lyrifissures, resulting from the discovery of *C. reticulatus,* indicates that it is h_1 and h_2 which are absent (Figs 16 & 18). Setae and lyrifissures are arranged more or less in the pattern seen in *C. reticulatus.* Differences occur in the number of pseudanal setae, there being three pairs in penthalodids, rhagidiids, *Benoinyssus* Fain, *Claveupodes* Strandtmann & Prasse, *Eupodes, Hawaiieupodes* Strandtmann & Goff and two pairs in *Caleupodes, Cocceupodes* and *Linopodes* Koch.

Acknowledgement

I would like to thank Professor G. O. Evans for his helpful criticisms of the manuscript.

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The *Barbus perince–Barbus neglectus* problem and a review of certain Nilotic small *Barbus* species (Teleostei, Cypriniformes, Cyprinidae)

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Introduction

The so-called small *Barbus* of Africa are a speciose group of cyprinid fishes loosely characterized by a relatively small adult size (mostly much less than 200 mm SL) and by the presence of radiating striae on the scales. They contrast with the large African *Barbus* which generally reach a larger adult size (mostly much greater than 200 mm SL) and have parallel or converging striae on the scales. However, this is a pragmatic segregation and monophyly for either group is not implied. Although the categories 'large' and 'small' *Barbus* form convenient groupings for the majority of species, there are species and species complexes that do not fit into either category. Exceptions include the complex of North African species with European affinities, some of the large species from the Cape region of South Africa (including *Barbus andrewi* Barnard, 1937 and *Barbus serra* Peters, 1864) and a few species between these geographical extremes (including *Barbus somereni* Boulenger, 1911 from the Ruwenzori region, *Barbus litamba* Keilhack, 1908 from Lake Malawi and *Barbus huloti* Banister, 1976 from Lake Albert).

Some small *Barbus species* are immaculate whereas others have variable patterns of spots and/or stripes. Intraspecific variability of colour pattern coupled, on occasion, with similar interspecific morphometric and meristic characters have made it very difficult to distinguish between species. Such is the case with the Nilotic species *Barbus perince* Rüppell, 1837 and *Barbus neglectus* Boulenger, 1903. As more specimens, possibly referable to either of these species, have become available it has proved increasingly difficult to attribute with confidence a specimen to either species.

This paper attempts to resolve this unsatisfactory state and to re-evaluate the status of some other Nilotic small *Barbus* species. It should be noted, however, that the conclusions apply *solely* to specimens from the Nile system. The status of specimens from elsewhere is uncertain as differences between these and Nilotic specimens have been detected but insufficient non-Nilotic material was available to evaluate their significance.

Barbus perince Rüppell, 1837

Barbus perince Rüppell, 1837 *Mus. senckenb.* **2:** 12.
Barbus neglectus Boulenger, 1903, *Ann. Mag. nat. Hist.* (7) **12:** 532.

Comments on the synonymy

(a) The identity of *Barbus perince* and the type specimen

Rüppell (1837) described the coloration of *Barbus perince* as (in translation) 'greenish on the back, silvery on the head and ventral regions with an inconspicuous blue streak'. There is no reference to spots on the flank and none are shown in his illustration (Fig. 1). The specimen described was stated to be no more than four inches (102 mm) long and with 31 scales in the lateral line. Despite subsequent statements, there is no evidence that Rüppell had more than one specimen. Much of his material is housed in the Senckenberg Museum, Frankfurt-am-Main, where specimen No. 851, collected at Cairo in 1834, is the only specimen dating from that time. This fish, 80 mm SL, is recognized as the holotype.

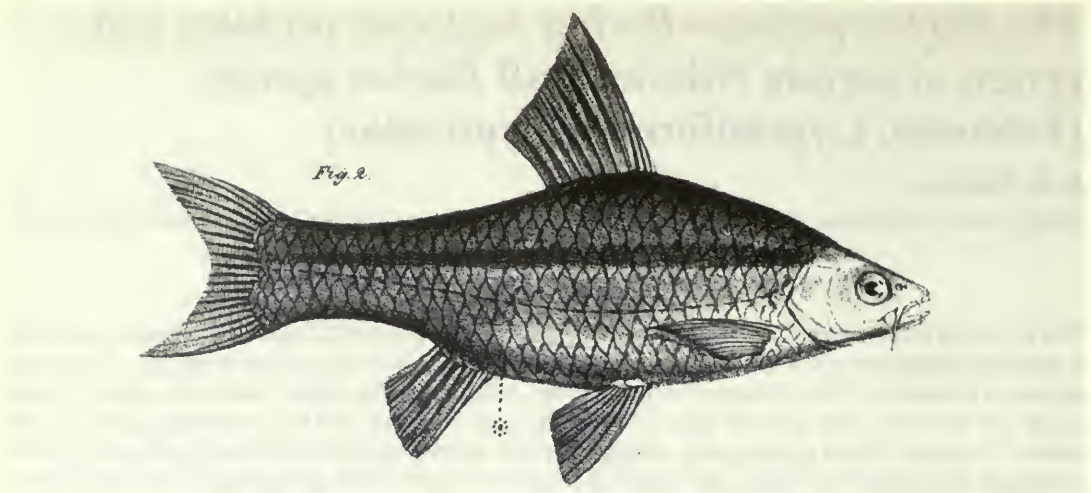

Fig. 1 *Barbus perince* from Rüppell, 1837. Original size.

Günther (1868: 105) gave a similar description based on nine specimens but with the comment '... sometimes with a small blackish spot on the root of the caudal'. Four specimens listed by Günther as 'a–b,c–d.Adult,Nile. From Dr Rüppell's collection', are registered in the BM(NH) collections as 1850.7.29:25–26 and 1860.11.9:115–116. The first lot was purchased from Rüppell; the second was presented by him. There is no indication in either the register or in Günther (1868) that they had type status. No other specimens listed by Günther were collected by, or associated with Rüppell. Günther (1869: 262) again gave a description of *Barbus perince* which scarcely differed from his previous one.

Boulenger (1907) gave an expanded description based on more specimens, many collected by Mr Loat between 1899 and 1902. He reported 'some specimens, and such are Rüppell's types from Cairo, are uniform silvery, with the back pale sea-green, the fins white and transparent. Others, and these seem to be by far the more frequent, have three more or less distinct round blackish spots on the middle of the side... Such specimens from the Damietta branch of the Nile, are thus described by Mr Loat:— "Silvery white, the fins colourless, or with a faint tinge of lemon on the dorsal and caudal, the back a dull brownish yellow, bordered below by a line of shot reddish gold, the three blackish spots are not visible when the fish is first taken out of the water, but appear a short time afterwards"...'. The specimen illustrated (Boulenger, 1907, plate 47, fig. 2) (Fig. 2) has three conspicuous spots. At the end of this description is '4, Nile at Cairo– Rüppell 1833 (Types)'. There is no reason why Boulenger should have considered these specimens to be types or to have been collected in 1833. Rüppell's letters in the BM(NH) archives show that the specimens accessioned in 1850 were caught by Rüppell in 1849 and sent to London directly from Egypt. The other alleged types were selected from Rüppell's private collection by Günther when he visited Frankfurt in 1860. None of these four specimens can therefore be considered to have type status.

Boulenger used his 1907 illustration again in the *Catalogue of the freshwater fishes of Africa* (Boulenger, 1911: 170). The accompanying description placed far more emphasis on the diagnostic value of the three 'more or less distinct round blackish spots on each side of the body, the first before, the second behind vertical of base of dorsal, the third at root of caudal'. It is this description that has been used by subsequent workers to determine a specimen as *Barbus perince*.

(b) Description of the holotype of *Barbus perince*

The overall body shape is well represented by Rüppell's original figure (reproduced here—Fig. 1) and that newly drawn from the holotype (Fig. 3). The fish is 80 mm SL and its measurements (expressed as a percentage of the SL) are: body depth = 32·5; head length = 23·8; eye diameter = 6·6;

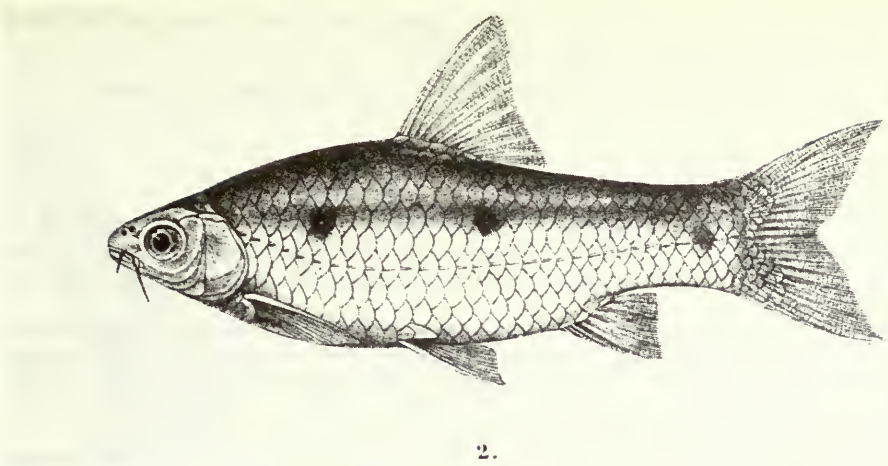

Fig. 2 *Barbus perince* from Boulenger's 'Fishes of the Nile' 1907 plate 47, Fig. 2. Original size.

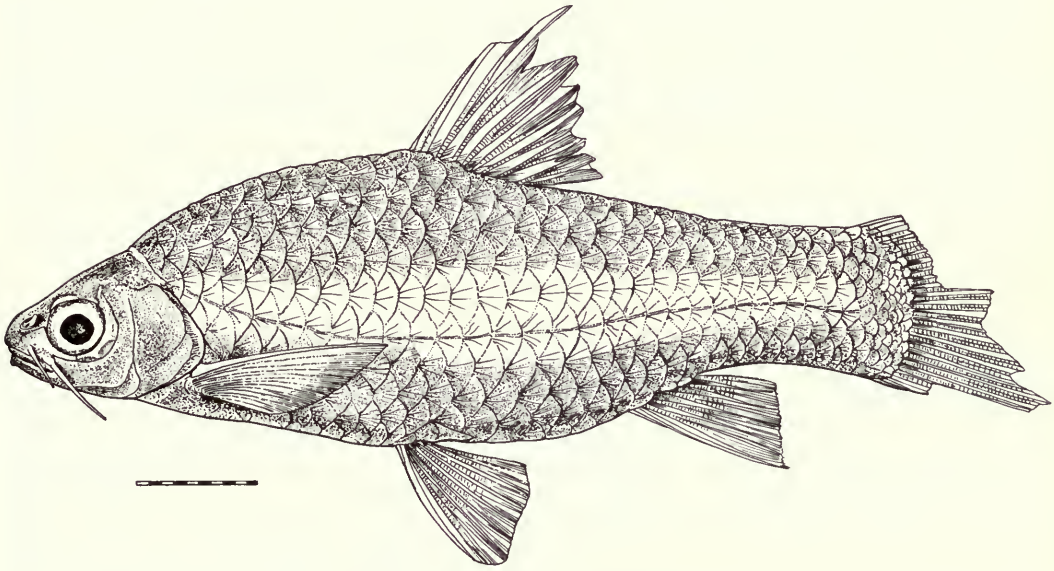

Fig. 3 *Barbus perince*, the holotype, 80 mm SL. ZMB 851. Drawn by Gordon Howes.

caudal peduncle length = 20·0; caudal peduncle depth = 16·2; pectoral fin length = 21·2; anterior barbel length = 3·7; posterior barbel length = 6·2. The origin of the dorsal fin is slightly in advance of the vertical from the pelvic fin origin. The dorsal fin has three unbranched and seven branched rays; the anal fin has three unbranched and five branched rays.

SQUAMATION. There are 29 scales in the lateral line (Rüppel's count of 31 lateral line scales included those extending onto the base of the caudal fin). The lateral line runs along the lower half of the caudal peduncle. There are $5\frac{1}{2}$ scale rows from the dorsal mid-line (immediately in front of the dorsal fin) to the lateral line and $4\frac{1}{2}$ from there to the ventral mid-line. Around the least circumference of the caudal peduncle there are 14 scales. The scales have few radiating striae and some scales, especially on the lower, posterior part of the body have reticulate foci. Although the foci resemble those of replacement scales (Neave, 1940) they occur too frequently on the individual (and in all specimens examined) for these scales to be replacement scales.

GILL RAKERS. There are seven widely and evenly spaced simple gill rakers on the first ceratobranchial, their shape exemplified by those in Fig. 16B.

COLORATION. The body colour is entirely pale and silvery. No dark spots are present.

(c) Other specimens previously given type status

There is no doubt that the four specimens Boulenger claimed to be types are conspecific with the holotype. These (BMNH 1850.7.29: 25–26 and 1860.11.9: 115–116, SL 65–74 mm) have the following characteristics. The proportional measurements are expressed as a percentage of the SL.

MORPHOMETRIC FEATURES. Body depth $\bar{x} = 34{\cdot}7$, range = 32·3–37·3; head length $\bar{x} = 23{\cdot}0$, range = 21·5–24·3; eye diameter $\bar{x} = 6{\cdot}2$, range = 5·9–6·7; caudal peduncle length $\bar{x} = 20{\cdot}6$, range = 20·3–21·5; caudal peduncle depth $\bar{x} = 15{\cdot}6$, range = 13·5–16·2; pectoral fin length $\bar{x} = 20{\cdot}6$, range = 19·4–20·9; anterior barbel length $\bar{x} = 3{\cdot}2$, range = 2·9–3·9; posterior barbel length $\bar{x} = 6{\cdot}2$, range = 5·4–7·6.

FINS. In the dorsal fin there are three (f3) or four (f1) unbranched rays and seven (f4) branched rays. The dorsal fin origin is slightly in advance of the vertical from the pelvic fin origin. The anal fin has three unbranched and five (f4) branched rays as do most small *Barbus* species.

SQUAMATION. There are 26 (f2), 27 (f1) or 28 (f1) scales in the lateral line, $5\frac{1}{2}$ scale rows from the dorsal mid-line (immediately in front of the dorsal fin) to the lateral line and $4\frac{1}{2}$ (f4) from that point to the ventral mid-line. Between the lateral line and the pelvic fin base there are $2\frac{1}{2}$ (f4) scales. Fourteen scales encircle the least circumference of the caudal peduncle. The scale striations and some foci are like those of the holotype (Fig. 4). The lateral line runs along the lower half of the caudal peduncle.

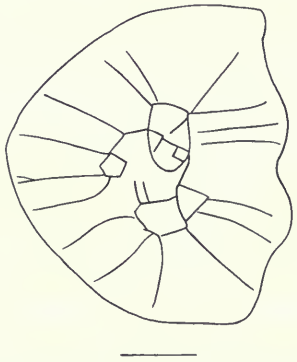

Fig. 4 A scale from one of the BM(NH) 'type' specimens of *Barbus perince*. SL 65 mm SL. Scale bar = 1 mm.

GILL RAKERS. There are 7 (f1) or 8 (f3) widely spaced gill rakers.

PHARYNGEAL BONES AND TEETH. The pharyngeal teeth number 2.3.5–5.3.2 and the rows are parallel (Fig. 5).

COLORATION. The fishes are entirely pale and silvery. No spots are present.

The species that has most often been confused with *Barbus perince* is *Barbus neglectus* which is discussed below.

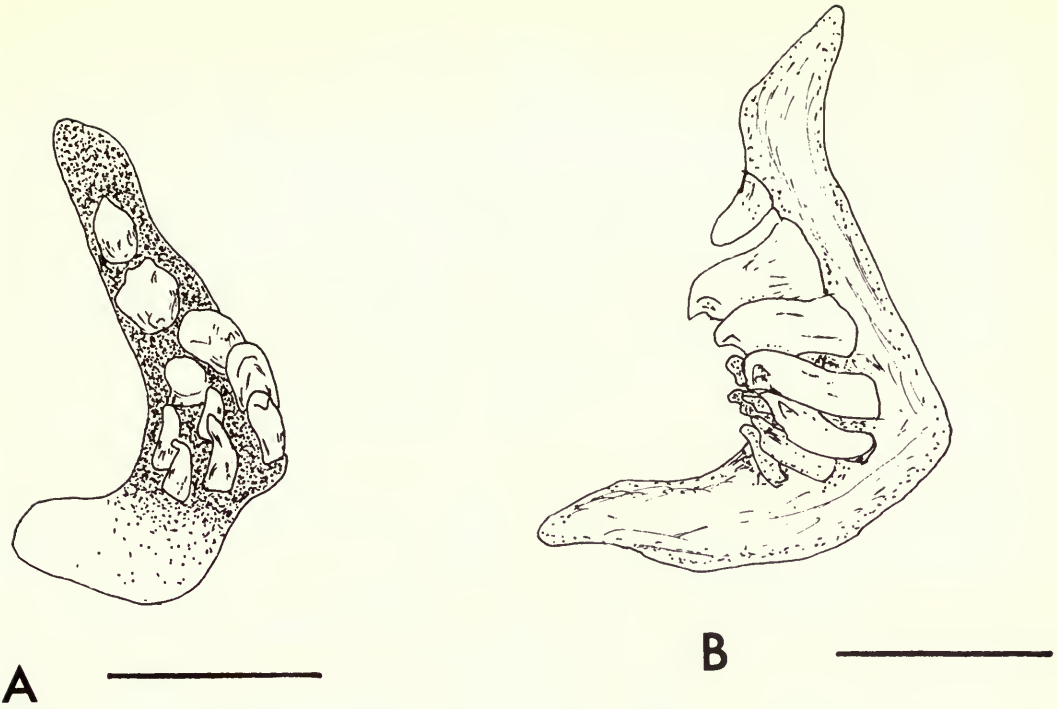

Fig. 5 A. Left pharyngeal bone of the 65 mm SL 'type' specimen of *Barbus perince* to show the alignment of the tooth rows. Scale bar = 2 mm. B. The same pharyngeal bone laid on its edentuluous surface. Scale bar = 2 mm.

(d) *Barbus neglectus* Boulenger, 1903

The original description was short, unillustrated and based on an unknown number of specimens. Specimens subsequently designated as syntypes by Boulenger (1911) were not registered until 1907 (1907.12.2: 1303–22 from Luxor; 1907.12.2: 1323–24 from Luxor to Assuam; 1907.12.2: 1327 from Ghat-el-Narua; all were collected by Loat). Neither the entries in the register nor the original labels on the bottles indicate that these are type specimens. Specimens registered before these (1905.10.26: 12–15 and 16–17) and collected by Flower from respectively, Rosaires and Wadi Medina, were never accorded type status. *Barbus neglectus* was illustrated and an enlarged description given by Boulenger (1907), (Fig. 6 here).

The sample from Luxor (1907.12.2: 1303–22) allegedly with twenty specimens actually contains 29, of which 26 match Boulenger's (1907) description and can be considered to be *Barbus neglectus*. The three other specimens are not *Barbus neglectus*, but their condition precludes their identification. (It should be noted that under-registering was a common practice at that time.) Two of the 26 *Barbus neglectus* specimens are of approximately the same total length (54 mm and 48 mm SL) that was quoted in the original description. One of these which matches the first illustration has been isolated, assigned the number 1907.12.2.: 1303, and is here designated as lectotype.

For ease of comparison with the holotype of *Barbus perince*, the lectotype (in parentheses) and the five largest paralectotypes are described; SL 42–48 mm (48). Measurements are expressed as a percentage of the SL. The corresponding data for non-type material are on p. 118.

MORPHOMETRIC FEATURES. Body depth $\bar{x}$ = 29·1, range = 27·8–30·2 (30·2); head length $\bar{x}$ = 23·6, range = 22·7–24·4 (24·0); eye diameter $\bar{x}$ = 7·8, range = 7·1–8·3 (8·3); caudal peduncle length $\bar{x}$ = 20·4, range = 19·6–21·3 (19·8); caudal peduncle depth $\bar{x}$ = 14·6, range = 14·0–16·0 (15·6); pectoral fin length $\bar{x}$ = 19·5, range = 17·8–22·2 (18·7); anterior barbel length $\bar{x}$ = 3·7, range = 2·3–5·2 (3·1); posterior barbel length $\bar{x}$ = 6·0, range = 3·1–6·6 (5·2).

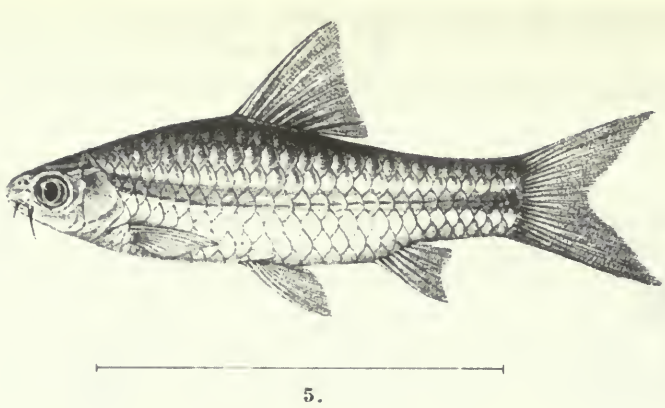

Fig. 6 *Barbus neglectus* from Boulenger's 'Fishes of the Nile' 1907 plate 47 Fig. 5. Original size.

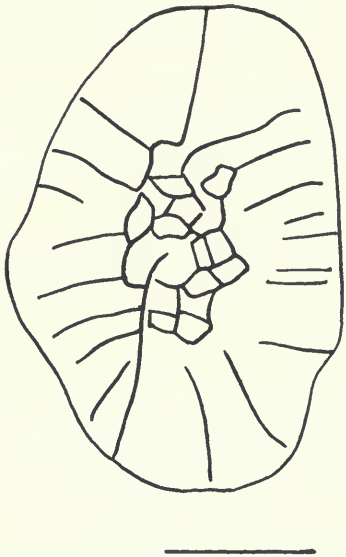

Fig. 7 A scale of the lectotype of *Barbus neglectus*. Scale bar = 1 mm.

The body shape is shown in Fig. 6.

FINS. The dorsal fin has three unbranched and 7 (f1) or 8 (f5) branched rays. Its origin is slightly in advance of the vertical from the pelvic fin insertion. The anal fin has three unbranched and five branched rays.

SQUAMATION. Lateral line with 24 (f2), 25 (f2), 26 (f1) or 27 (f1) scales; $3\frac{1}{2}$ (f5) or $4\frac{1}{2}$ (f1) ($3\frac{1}{2}$) scale rows from the dorsal mid-line (in front of the dorsal fin origin) to the lateral line and $3\frac{1}{2}$ (f5) or $4\frac{1}{2}$ (f1) ($3\frac{1}{2}$) from the lateral line to the ventral mid-line. Between the lateral line and the pelvic fin base there are 2 (f5) or $2\frac{1}{2}$ (f1) (2) scale rows. Twelve scales (f6) encircle the least circumference of the caudal peduncle.

The scales (Fig. 7) bear few radiating striae and many have a reticulate focus, especially those on the lower, posterior part of the body.

GILL RAKERS. There are 8 (f3) or 9 (f3) short, broad, widely spaced gill rakers on the first ceratobranchial.

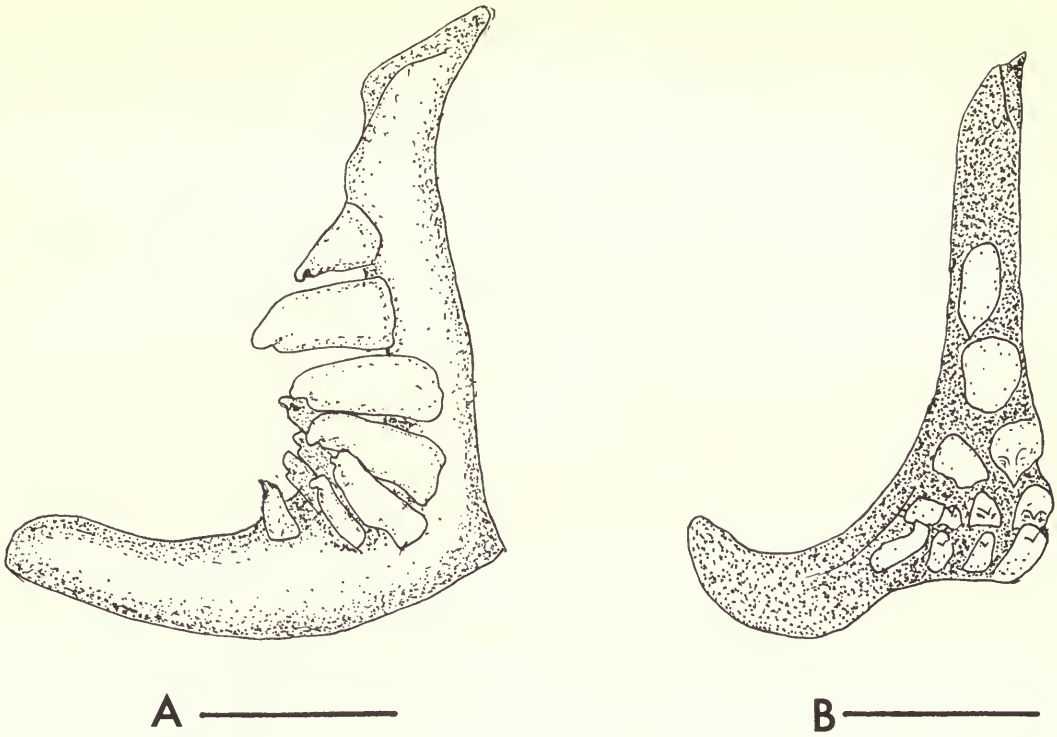

Fig. 8 A. Left pharyngeal bone of the largest paralectotype of *Barbus neglectus*, lying on its edentuluous surface. Scale bar = 1 mm. B. The same pharyngeal bone positioned to show the alignment of the tooth rows. Scale bar = 1 mm.

PHARYNGEAL BONES AND TEETH. The left pharyngeal bone of the large paralectotype is atypical in possessing 4 rows of teeth (1.2.3.5) (Figs 8A & 8B). In all other respects, the teeth and the rows are the same as those of *Barbus perince* shown in Figs 5A & 5B. In three other specimens examined, the single tooth of the fourth row is absent.

COLORATION. The body is silvery brown and devoid of spots.

Discussion

In Boulenger (1911) the main diagnostic differences between *Barbus perince* and *Barbus neglectus* are that the body of the former is deeper and that larger fishes (usually identified as *Barbus perince* in museum collections) tend to have 14 circumpeduncular scales compared with 12 in smaller specimens (which were referred to *Barbus neglectus*). This increase in scale number with growth will be discussed in a separate publication.

The similar meristic and morphometric data (allowing for allometry e.g. the deeper body in larger specimens), and the frequent presence of reticulate foci on the scales, indicate that *Barbus neglectus* is conspecific with *Barbus perince*. Indeed, if smaller specimens (previously identified as *Barbus neglectus* in the BM(NH) collections) are arranged in size series with larger specimens (i.e. *Barbus perince*) a morphometric continuum is established and the differences recorded by Boulenger (1911) are no longer significant.

Barbus perince is normally a silvery fish; only a small proportion (32 out of 145 specimens) have any spots. When present, the spots are faint but their position is important in distinguishing spotted *Barbus perince* specimens from the species described below. The first spot, about the size of a scale, lies over the overlap of the sixth and seventh scales of the row above the lateral line and extends onto the scale dorsal to this overlap. The second spot is in a similar position eight scales

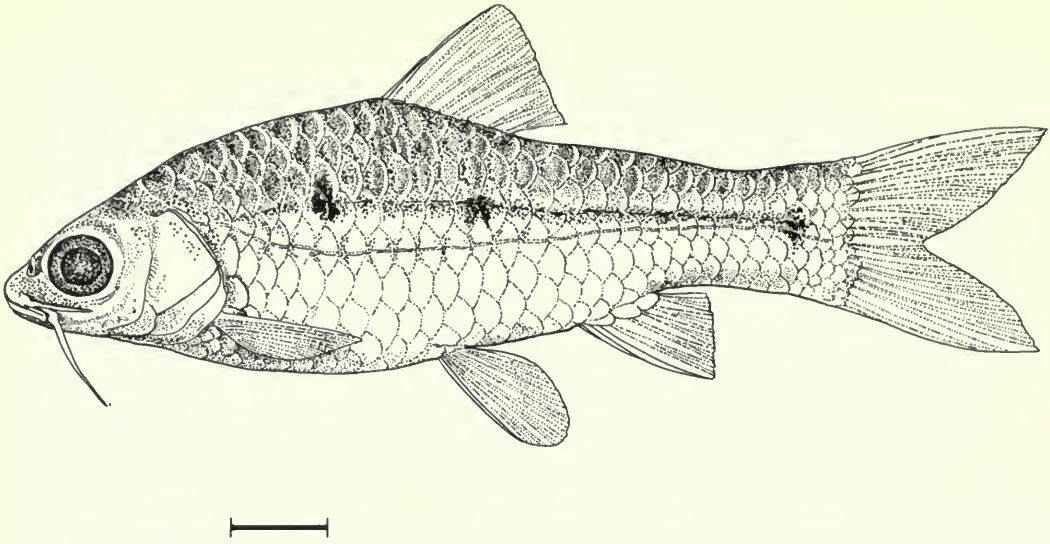

Fig. 9 An example of the heavily spotted species formerly confused with *Barbus perince*. Drawn by Gordon Howes. Scale bar = 5 mm.

beyond the first on the same row and *behind* the vertical from the base of the last dorsal fin ray. The third spot lies mostly on the lateral line scale immediately behind the point of caudal flexure. In all the specimens with spots, that on the caudal peduncle is always present; in four specimens it is the only one present. Fifteen specimens have just the first and third spots, and thirteen have all three spots.

Once it is accepted that only about 25% of the specimens of *Barbus perince* have spots, the question of the identity of the other spotted specimens previously identified in museum collections as *Barbus perince* and *Barbus neglectus* is raised. It is argued below that these spotted fishes (Fig. 9) may be *Barbus stigmatopygus*, hitherto only known as a very small fish.

Barbus stigmatopygus Boulenger, 1903

Barbus stigmatopygus Boulenger, 1903 *Ann. Mag. nat. Hist* (7) **12:** 533.
Barbus miolepis Boulenger, 1903 *Ann. Mag. nat. Hist.* (7) **12:** 533. (*nec* Boulenger, 1902 *Annls Mus. r. Congo Belge* **2:** 32).
Barbus werneri Boulenger, 1905 *Proc. zool. Soc. Long.* **1:** 63.
Barbus alberti Poll. 1939 *Explor. Parc natn. Albert Miss G. F. de Witte* **24:** 28.

Notes on the synonymy

(a) ***Barbus stigmatopygus***

From the time of Boulenger's brief original description (1903) and his enlarged redescription (1907) *Barbus stigmatopygus* has been diagnosed as a species reaching a very small adult size (24 mm total length), without an enlarged unbranched ray in the dorsal fin, without barbels and with only the anterior scales of the lateral line having pores (Boulenger, 1911; Sandon, 1950). However, Boulenger was in error regarding the barbels. Of the eight syntypes [BM(NH) 1907.12.2: 1255–60], SL 20 (f2), 19, 16, 15 (f2) and 14 (f2) mm, the three largest have a pair of posterior barbels respectively 1·0 (f2) and 0·6 mm long. There is no sign of the anterior barbels, but the specimens are in poor condition and may at some time have been partially dried.

Morphometric and meristic characters of the six largest syntypes are given below. The other two syntypes are too soft and damaged to provide any useful data. All proportional measurements are expressed as a percentage of the standard length.

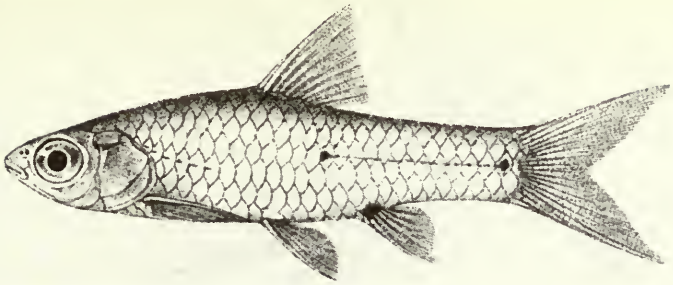

Fig. 10 *Barbus stigmatopygus*, a syntype from Boulenger's 'Fishes of the Nile' 1907 plate 47 Fig. 8. Original size.

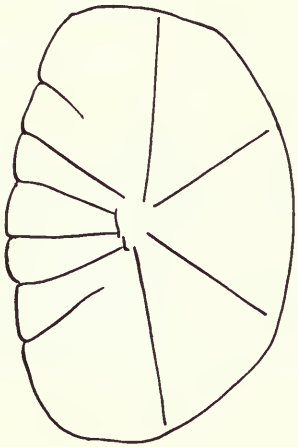

Fig. 11 A scale from a syntype of *Barbus stigmatopygus*. Scale bar = 0·5 mm.

MORPHOMETRIC FEATURES. Body depth $\bar{x} = 27{\cdot}0$, range 25·0–28·6; head length $\bar{x} = 26{\cdot}7$, range = 24·7–28·4; eye diameter (n = 5) $\bar{x} = 9{\cdot}3$, range = 9·0–10·0; pectoral fin length $\bar{x} = 19{\cdot}8$, range = 18·0–21·0; caudal peduncle length $\bar{x} = 21{\cdot}6$, range = 20·5–24·0; caudal peduncle depth $\bar{x} = 13{\cdot}5$, range = 11·9–15·0; posterior barbel length (n = 3) $\bar{x} = 4{\cdot}4$, range = 3·2–5·0.

FINS. The dorsal fin has 3 unbranched and 7 (f1) or 8 (f5) branched rays. The last unbranched ray is neither stiffened nor enlarged. The anal fin has three unbranched and five branched rays in all specimens.

SQUAMATION. In the four syntypes from which lateral scale counts were obtainable there are 23 (f2) or 24 (f2) scales in the line of which the first 5 (f2) or 6 (f2) are pored. Around the least circumference of the caudal peduncle there are 10 (f4), 11 (f1) or 12 (f1) scales. The scale shape and distribution of the striae are shown in Fig. 11.

GILL RAKERS. Of particular note are the low number and the arrangement of the gill rakers (Fig. 12). There are only 2 (f2) conspicuous gill rakers situated on the dorsal part of the first ceratobranchial close to the angle with the epibranchial. The ventral half of the bone is covered with an irregularly papillate tissue (see. p. 126).

PHARYNGEAL BONES AND TEETH. The pharyngeal bone has recurved, hooked pharyngeal teeth arranged in three rows numbering 2.3.5–5.3.2. The two teeth of the outer row are not parallel with the middle row (see p. 118).

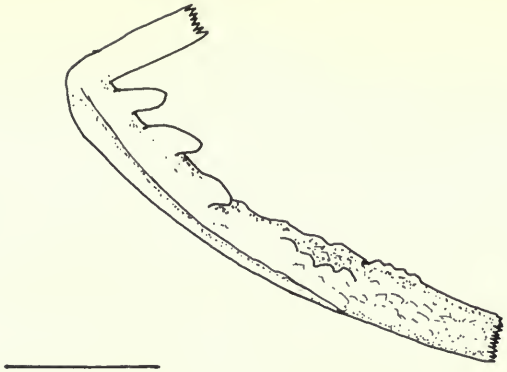

Fig. 12 The gill rakers on the first ceratobranchial of a syntype of *Barbus stigmatopygus*. Scale bar = 0·5 mm.

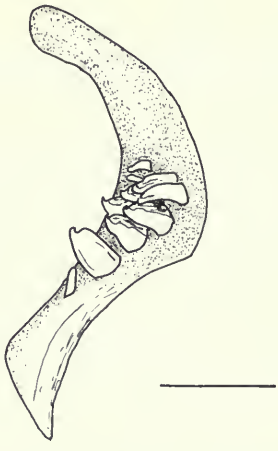

Fig. 13 A pharyngeal bone from a syntype of *Barbus stigmatopygus* Scale bar = 0·5 mm.

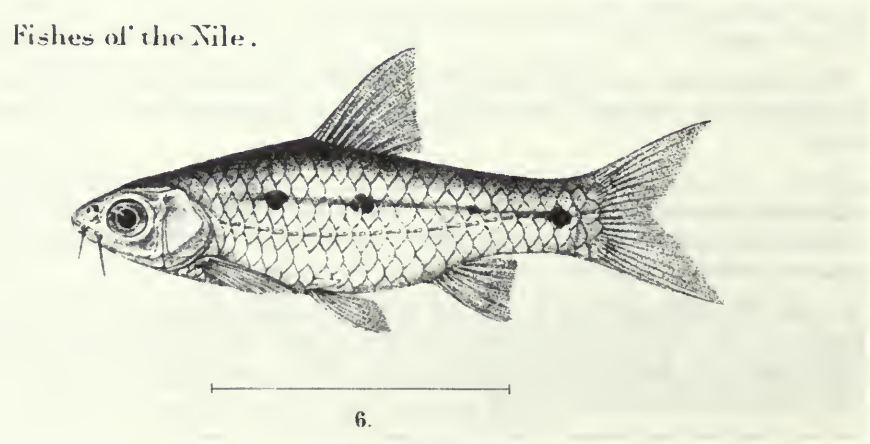

Fig. 14 One of the syntypes of *Barbus werneri* from Boulenger's 'Fishes of the Nile' 1907 plate 47 Fig. 6. Original size.

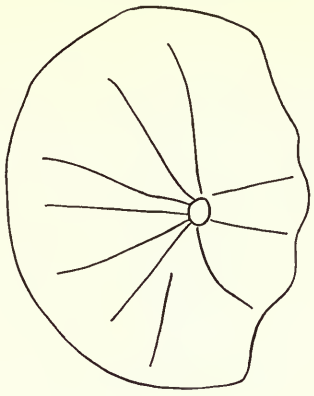

Fig. 15 A scale from the headless syntype of *Barbus werneri*. Scale bar = 1 mm.

COLORATION. Although the syntypes have the relative uniformity of colour caused by long storage in alcohol and have lost many anterior scales, a pigmentation pattern can be discerned. There are three dark spots, each about the size of a scale, on the flanks. The first spot lies in the same relative position in all specimens but in only one can it be confirmed as at the level of the overlap of the seventh and eighth scales in the row above the lateral line. The second spot is on the 6th–7th (f2) or the 7th–8th (f1) scale behind the first and lies on or in front of the vertical from the last dorsal fin ray. The third spot is situated on the caudal peduncle at the caudal flexure. The two posterior flank spots may be joined by a thin dark line. There is also a small dark spot at the base of the anterior anal fin rays.

(b) **Barbus werneri**

Barbus werneri is a replacement name for *Barbus miolepis* Boulenger, 1903 preoccupied by *Barbus miolepis* Boulenger, 1902 a Congo species with a serrated and spinous last unbranched dorsal fin ray. Boulenger (1905: 63) realized his error in proposing a homonym and used the name *'werneri'* for the Nilotic *'miolepis'* but confusingly dated that name as 1893. I have been unable to find any paper in 1893 dealing with Nilotic fishes. Indeed in Boulenger's own annotated bibliography (Boulenger, 1921) the Congo *miolepis* is dated as 1902 and no relevant article is listed for 1893. One must therefore assume that the 1893 attribution was a *lapsus*. It should be noted that the figure of the 'true' *miolepis* in Boulenger (1911 fig. 117) has been transposed with fig. 131 where it is captioned as *Barbus humeralis*.

In the original description of *Barbus miolepis* Boulenger (1903) did not state how many specimens he examined. In 1907 he listed the types as coming from four localities: these are 1907.12.2: 1328–32, Lake No, White Nile; 1907.12.2: 1333, Fashoda, White Nile; 1907.12.2: 1934, Kaka, White Nile and 1907.12.2: 1335 Gondokoro, Bahr-el-Gebel. Most are in poor condition and only three specimens (i.e. 1907.12.2: 1334 and two in 1907.12.2: 1328–32 are sufficiently well-preserved to provide meristic and morphometric data.

The morphometric characteristics of the three well-preserved syntypes, fishes of 26, 29 and 30 mm SL are given below. All measurements are expressed as a percentage of the standard length.

MORPHOMETRIC CHARACTERISTICS. The body shape is shown in Fig. 16.
Body depth $\bar{x} = 28{\cdot}7$, range = 26·9–31·0; head length $\bar{x} = 27{\cdot}0$, range = 26·6–27·6; eye diameter $\bar{x} = 9{\cdot}1$, range = 8·0–9·6; caudal peduncle length $\bar{x} = 18{\cdot}9$, range = 18·4–19·6; caudal peduncle depth $\bar{x} = 14{\cdot}8$, range = 13·8–15·5; pectoral fin length $\bar{x} = 20{\cdot}0$, range = 18·3–21·1; anterior barbel length $\bar{x} = 8{\cdot}1$, range = 7·7–8·3; posterior barbel length $\bar{x} = 10{\cdot}1$, range = 9·2–11·7. The barbels are conspicuously long, the anterior, when entire, reaching to below the centre of the eye, and the posterior almost to the angle of the preoperculum.

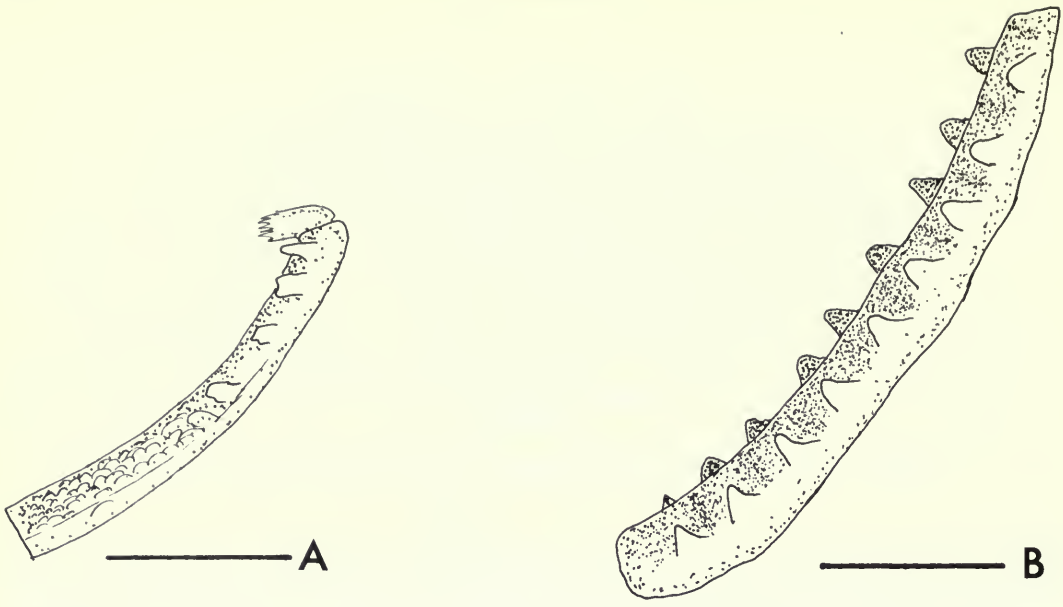

Fig. 16 A. The first ceratobranchial of the headless syntype of *Barbus werneri*. Scale bar = 1 mm. B. For comparison, the first ceratobranchial of *Barbus perince* to show the normal condition of the gill rakers in small *Barbus* species. Scale bar = 1 mm.

FINS. The dorsal fin has 3 (f6) unbranched and 7 (f1) or 8 (f5) branched rays. The anal fin has 3 unbranched and 5 branched rays (f6).

SQUAMATION. The lateral line series has 24 (f2), 25 (f2) or 26 (f2) scales. There are $4\frac{1}{2}$ (f6) scale rows from the dorsal mid-line to the lateral line and $3\frac{1}{2}$ (f1) or $4\frac{1}{2}$ (f5) from the lateral line to the ventral mid-line. Twelve scales encircle the least circumference of the caudal peduncle (f6). The scales have few radiating striae.

GILL RAKERS. The first ceratobranchial has the same arrangement of gill rakers seen in the syntypes of *Barbus stigmatopygus* (Fig. 16A). There are two large and one small gill rakers dorsally. The ventral part of the bone is covered with irregularly papillate tissue. Very small, widely spaced ridges, of unknown homology are present below this tissue. The ventral ridges were not detected in the very small syntypes of *Barbus stigmatopygus*. This configuration of gill rakers is contrasted with the modal condition in small *Barbus* in Fig. 16B.

PHARYNGEAL BONES AND TEETH. The pharyngeal bones were removed from a badly damaged syntype of about 30 mm SL (ex 1907.12.2: 1328–32). They have a 2.3.5–5.3.2 tooth arrangement (Fig. 17). The teeth of the outer row are not parallel with the middle row. This can be seen from the position of the crowns but could not be illustrated as attempts to clear the residual tissue from between the teeth destroyed the bone.

COLORATION. Seven syntypes have markings consisting of 5(f2), 4 (f3) or 3 (f2) dark spots. The first spot is very small and on the fourth scale of the row above the lateral line. The second spot is larger, about the size of a scale and is at the overlap of the sixth and seventh (f1) or seventh and eighth (f6) scale of the same row and the scale dorsally between them. Like the second spot, the third is at the level of the horizontal septum and lies on, or before, the vertical from the base of the last dorsal fin ray. The fourth spot is very small and is situated five scales caudad to the third spot in the same scale row. The fifth spot is visible between the second and third pored-scales from the posterior end of the lateral line. The second, third and fifth spots present in all these specimens, correspond in position to those of *Barbus stigmatopygus*.

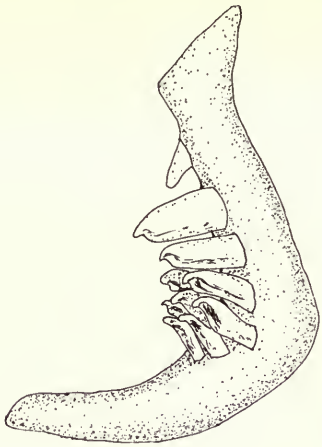

Fig. 17 A reconstruction of the left pharyngeal bone of the headless syntype of *Barbus werneri*. The bone was accidentally destroyed in the later stages of preparation. Scale bar = 0·5 mm.

In the smaller syntypes there is some weak pigmentation at the base of the anal fin. This is missing in the larger specimens but a thin, weak line of pigment is present between the posterior spots.

The body colour is brown, darker dorsally. The fins are colourless.

Discussion

The paucity of gill rakers and the presence of papillate tissue on the ventral part of the first ceratobranchial (p. 126), the disposition of the pharyngeal teeth (p. 127) and the position of the spots on the flank are characters sufficiently diagnostic to consider *Barbus werneri* to be conspecific with *Barbus stigmatopygus*.

(c) *Barbus alberti*

Barbus alberti is a largely overlooked species from the Lake Edward drainage (Rutshuru river, Poll, 1939). Poll (op. cit.) reported the three syntypes to be in extremely poor condition and that scale counts were very difficult to obtain. The only scale count he gives, that of the lateral line, is higher than that recorded here for *Barbus stigmatopygus* (31 *cf.* 24–26) but Poll does not state where he terminated this count. I have not been able to examine the syntypes but the long barbels and general body shape are clear in fig. 9 of Poll (1939), the body spots less so. However, I consider these features to be sufficiently diagnostic to regard *Barbus alberti* as conspecific with *Barbus stigmatopygus*. The apparent differences between these nominal species are discussed below, following a redescription of *Barbus stigmatopygus*.

Redescription of *Barbus stigmatopygus*

A sample of 24 *Barbus stigmatopygus* covering the size range extending from the types of *Barbus werneri* to the largest available specimens (i.e. 26–54 mm SL) forms the basis of this redescription. All proportional measurements are expressed as a percentage of the standard length.

MORPHOMETRIC FEATURES. Body depth $\bar{x} = 31{\cdot}3$, range = 26·9–34·7; head length $\bar{x} = 27{\cdot}4$, range = 25·5–34·7; eye diameter $\bar{x} = 8{\cdot}4$, range = 6·9–10·4; caudal peduncle length $\bar{x} = 20{\cdot}8$, range = 19·5–25·0; caudal peduncle depth $\bar{x} = 14{\cdot}1$, range = 12·3–15·9; pectoral fin length $\bar{x} = 19{\cdot}7$, range = 17·0–21·2; anterior barbel length $\bar{x} = 8{\cdot}4$, range = 7·2–9·5; posterior barbel length $\bar{x} = 11{\cdot}6$, range = 9·2–13·1.

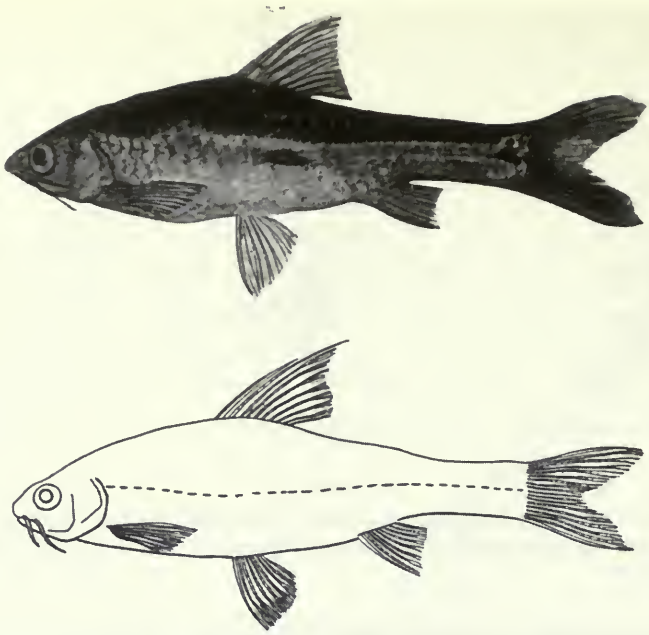

FIG. 9. — *Barbus alberti* sp. n. (riv. Rutshuru).
Longueur : 95 mm.

Fig. 18 *Barbus alberti* from Poll, 1939. Original size.

The long barbels are particularly noteworthy. The posterior barbel extends to, or beyond, the angle of the preoperculum and the anterior one to, or beyond, a vertical through the middle of the eye (Fig. 9).

FINS. The dorsal fin has three unbranched and 7 (f4) or 8 (f20) branched rays. The anal fin has three unbranched and five branched rays (f24).

SQUAMATION. In the lateral line series there are 24 (f2), 25 (f8) or 26 (f14) scales. All the specimens examined have $4\frac{1}{2}$ scale rows between the lateral line and, respectively, the dorsal and ventral midlines, and $2\frac{1}{2}$ scale rows from the lateral line to the insertion of the pelvic fin. Twelve scales encircle the least circumference of the caudal peduncle. The scales have a few radiating striae and a clear focus (Fig. 19). The lateral line runs on the middle of the side of the caudal peduncle.

GILL RAKERS. In 12 specimens examined there are 2 (f1), 3 (f10) or 4 (f1) large gill rakers on the dorsal half of the first ceratobranchial; of these, the one or two nearest the epibranchial are larger than the rest. The lower half of the ceratobranchial is covered with a papillate tissue under which are 0 (f2), 1 (F2), 2 (f5) or 3 (f3) low ridges or protuberances of uncertain homology.

PHARYNGEAL BONES AND TEETH. A pharyngeal bone is shown in Fig. 21. The teeth are arranged in three rows of 2.3.5–5.3.2 teeth. The two teeth of the outer row are characteristically close together and not parallel to the middle row; rather, they, and the first tooth of the middle row appear to form a diagonal row. This, and the tooth form can be seen in Fig. 21.

COLORATION. Most specimens have three lateral spots, but some have up to five and others only two. Irrespective of the number of spots, a line of dark brown pigment is present and may join the middle and posterior spots, and sometimes joins all. The spots are usually just smaller than the scales. The first spot is at the overlap of the seventh and eighth scales of the row above the lateral line and the scale dorsally between them. The third spot, when present, is usually 6 or 7 scales caudad to the first spot and lies on, or in front of, the vertical from the base of the last dorsal fin ray.

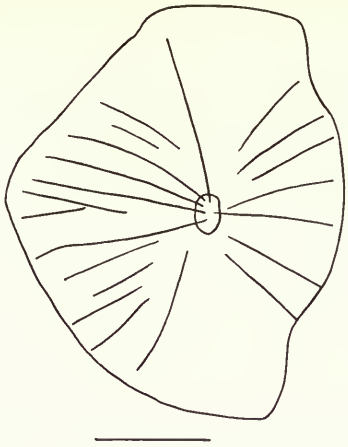

Fig. 19 A scale from the specimen shown in Fig. 9. Scale bar = 1 mm.

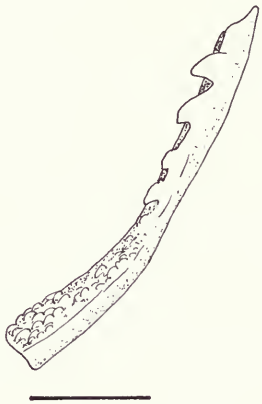

Fig. 20 The first ceratobranchial from a 50 mm SL specimen of the species shown in Fig. 9. Scale bar = 1 mm.

The fifth spot lies between the second and third pored-scales from the posterior end of the lateral line. The second and fourth spots are much smaller and correspond to the positions described for those in *Barbus werneri*.

The body colour is yellow-brown to brown, darker on the back than on the ventral surface, with the pigment intensified on the posterior part of the exposed section of the dorsal scales. There is no silvery, reflective sheen as there is in *Barbus perince*.

Discussion

The common possession of a few large gill rakers on the upper part of the first ceratobranchial, papillate tissue on the lower part, the alignment of the pharyngeal tooth rows and the position of the flank spots, appears to justify considering *Barbus stigmatopygus, Barbus werneri* and *Barbus alberti* as conspecific despite seeming contradictions in the colour pattern, the number of pored scales in the lateral line and the number of barbels. These apparent anomalies are discussed below.

(d) Comments on the pigmentation pattern

Hitherto, the main difference in pattern noted between *Barbus stigmatopygus* and *Barbus werneri* (see Boulenger, 1911) is the presence of a small black spot at the base of the anal fin in *Barbus*

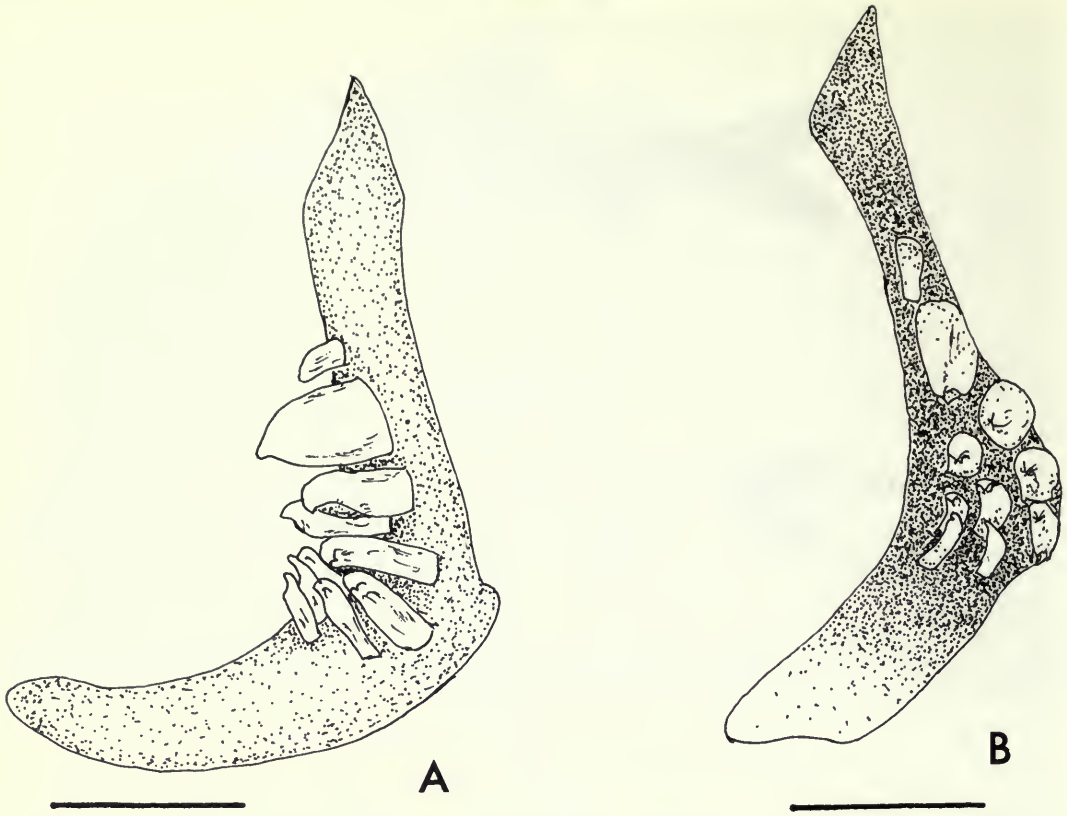

Fig. 21 A. The left pharyngeal bone of a 50 mm SL specimen of the species shown in Fig. 9. Scale bar = 1 mm. B. The same pharyngeal bone positioned to show the alignment of the tooth rows. Scale bar = 1 mm.

stigmatopygus. The pigment is only partly superficial. In small (juvenile) fishes the densest concentration of melanophores lies in the muscles at the base of the anal fin and is visible through the thin layer of translucent skin. With growth, the superficial melanophores disappear. Those in the anal fin muscles remain but become less dense and are no longer visible through the tissue.

Such deeper pigmentation in various young cyprinid fishes has been noted by Balinsky (1948) and Kortmulder & Van der Poll (1981). In a staged growth series of *Barbus stigmatopygus* from seasonal pools in the Sudd (1985.1.29: 64–83 and 84–98; 14–50 mm SL) the anal fin spot becomes faint at about 18–20 mm SL. It is not usually visible in fishes larger than 23 mm SL. However, the internal pigmentation is still present in specimens over 40 mm SL.

The anal fin spot has been shown to be a juvenile character in other cyprinid species e.g. *Barbus binotatus* Valenciennes 1842 (Weber & de Beaufort, 1916: 188).

The variation in pigmentation pattern, especially the anal fin spot, formerly used in distinguishing these species, is thus no more than an ontogenetic feature.

(e) The lateral line tubules

Little has been published on the development of the pores of lateral line scales. Scale formation frequently starts at the lateral line (Neave, 1940) but there is no information on whether the tubule forms concurrently with the growing scale or whether it is a later development.

Mori (1931*a*, 1931*b*) studied the formation of the lateral line tubule formation in transplanted scales on the goldfish (*Carassius autatus* (L.1758)). He found that in ordinary scales transplanted

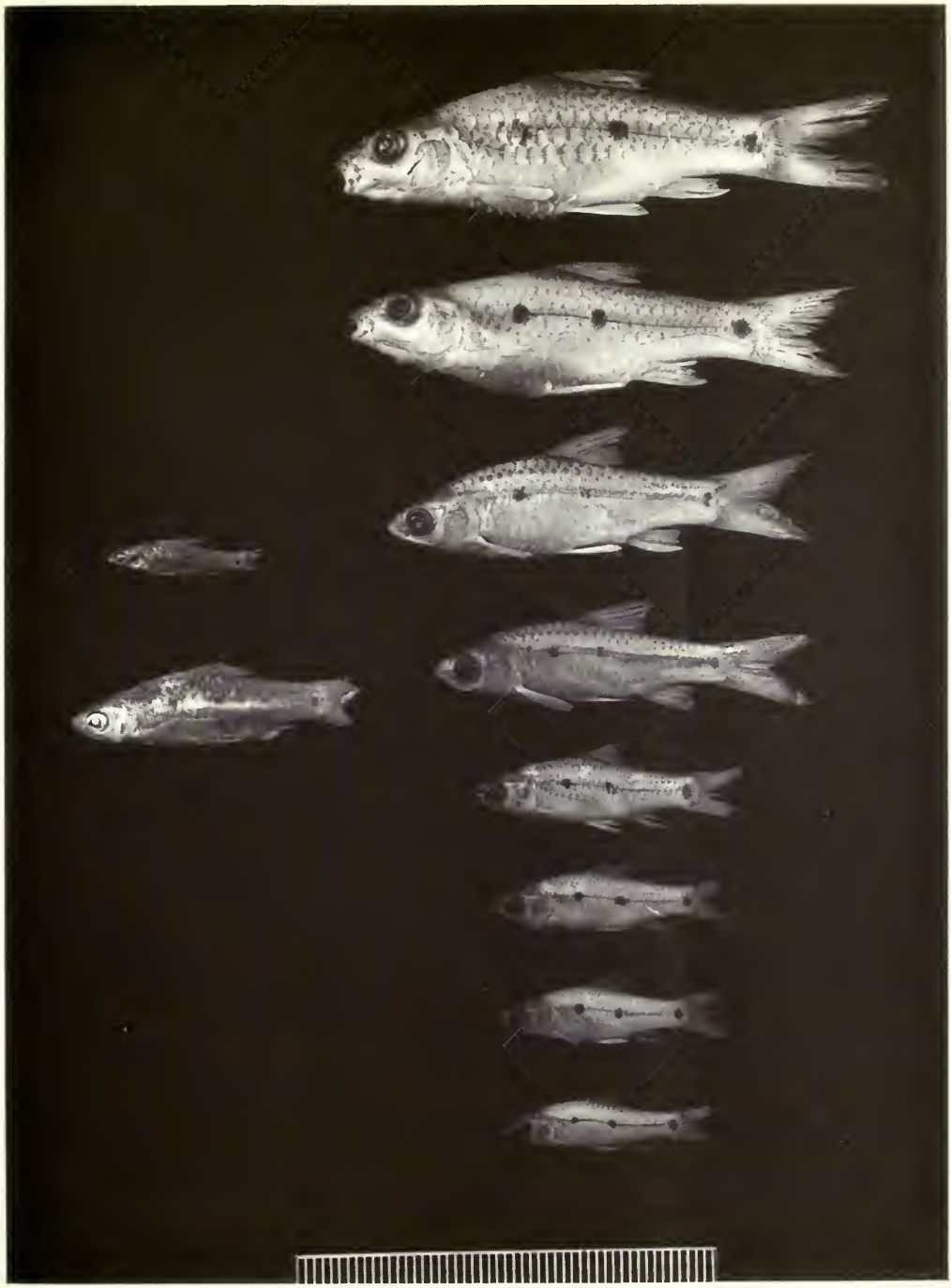

Fig. 22 Growth stages of *Barbus stigmatopygus*. A syntype is at the top left and a syntype of *Barbus werneri* below it.

into lateral line scale pockets from which the scales had been removed they only developed the pore after the canal from the preceding scale had grown backwards beneath the transplanted scale and the lateral line organ had developed. Whether this method of pore formation occurs in ontogeny is unknown.

In the east African species *Barbus neumayeri* (Fischer, 1884) scales become distinguishable in specimens between 10 and 20 mm SL, tubules are detectable in the better formed lateral line scales at less than 20 mm SL and a full complement is present at 22 mm SL (Banister, 1980). The smallest specimen of *Barbus stigmatopygus* available to me is 12 mm SL; it is fully scaled, but its poor condition precludes the detection of tubules in the lateral line scales. Specimens of 14 mm SL have 4, 5 or 6 scales with well defined tubules (as in the 15–20 mm SL syntypes). Specimens of more than 20 mm SL have pores in all the lateral line scales. The anterior few pored scales appear much earlier than the others, but, to judge by the small size differences between specimens with only the anterior set of pores and those with a full complement, the posterior pores develop extremely rapidly. The posterior pores first appear as a shallow groove in scales which continue the horizontal series of anterior tubule-bearing scales caudad. The groove runs from the middle of the scale to the posterior margin where the edge of the scale is notched. In two specimens (19·0 and 19·5 mm SL ex 1985.1.24: 84–98) there is no perforation in these scales. In the same lot there is a slightly larger fish (20·0 mm SL) in which the edges of the groove are raised, whilst in a fish of 20·5 mm SL the leading scales of the posterior row series have the groove roofed over, leaving a pore posteriorly. In a specimen of 23·5 mm SL only the last two lateral line scales are incompletely roofed over, a long posterior slit persisting. At 50 mm SL the only discernable differences between the anterior and posterior series of the lateral line tubules is that the former are slightly wider and the lateral wall of the tube is thicker.

The number of barbels

As now defined, *Barbus stigmatopygus* contains fishes with 0, 2 or 4 barbels. In the syntypic series, posterior barbels are detectable in 3 specimens longer than 19 mm SL. The smaller fishes are without barbels, although, as noted earlier, the likelihood of seeing them in such poorly preserved material is remote.

In specimens recently collected in the Sudd (1985.1.29: 64–83), the posterior barbel becomes visible as a small protuberance in fishes of about 14 mm SL. Thereafter, barbel growth is rapid (Fig. 23); in fishes of 16 mm SL, the posterior barbel is about 0·15 mm long, at 20 mm SL 1·2 mm long, and at 27 mm SL 2·1 mm long. The anterior barbel first appears at about 20 mm SL and its subsequent growth is also rapid. In adults the barbels are characteristically long (see p. 128).

In another sample from further north in Sudan (Tira Mandi, 10°54′N, 30°30′E and Umm Jan, 11°20′N, 30°31′E—both localities are included in 1948.1.14: 83–121, 10–34 mm SL) the posterior barbels appear at about 14 mm SL and the anterior ones at about 17 mm SL.

It has been argued (Banister, 1980) that too much reliance has been placed on the use of barbels in barbine classification. *Barbus stigmatopygus* is yet another reason why the Schultz (1957) classification of barbines into genera with, respectively, 4, 2, or 0 barbels is untenable.

In the case of *Barbus amboseli* Banister, 1980 which has a similarly delayed barbel development, I suggested that the number of barbels might be related to the sex of the fish as is the case in some populations of *Barbus anoplus* Weber, 1897 (Jubb, 1967). I can add nothing to the arguments for *B. amboseli* as no new specimens are available, but in *B. stigmatopygus* there is no link between barbel development and sex; the barbels simply develop later than in many other species, although earlier than in *B. amboseli* where the anterior barbels start to form at about 35 mm SL. The largest known specimen of *Barbus amboseli* is 45 mm SL *cf* 54 mm SL for *Barbus stigmatopygus*.

Redescription of *Barbus tongaensis* Rendahl, 1935

The collection made by Dr R. G. Bailey in the Sudd contained 40 specimens of this species which was previously known only from the holotype. An expanded description is therefore given below.

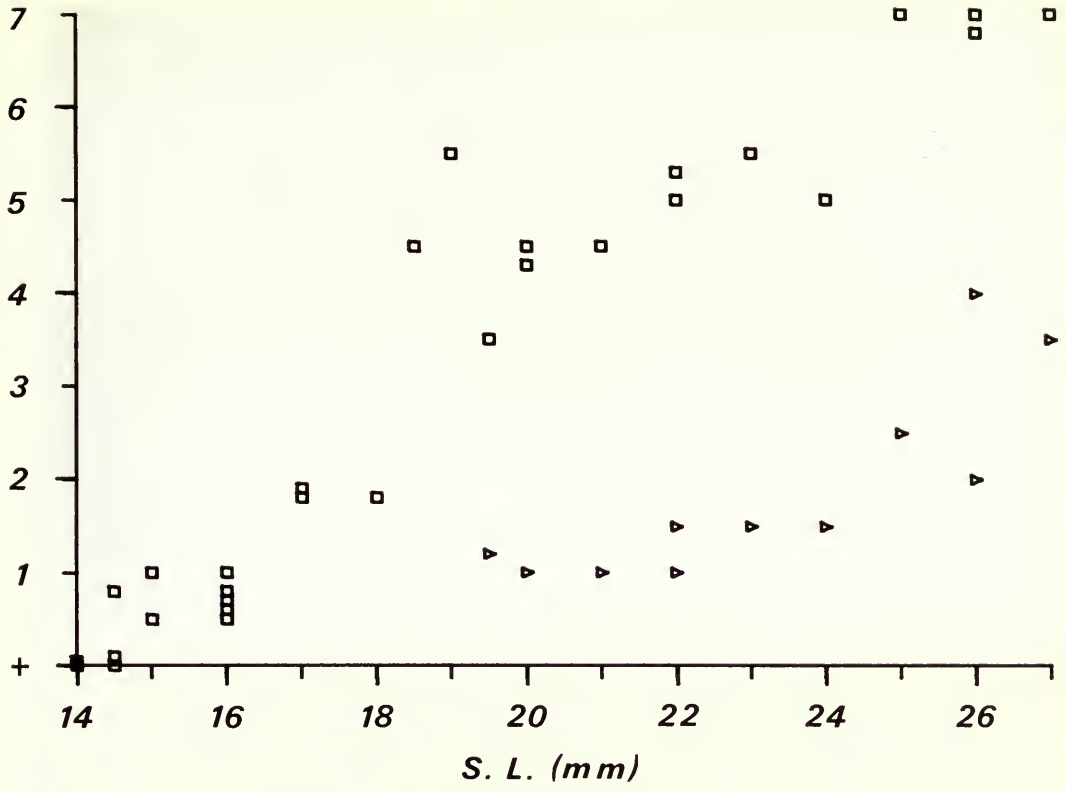

Fig. 23 Barbel growth in *Barbus stigmatopygus*. ▷ = anterior barbel, □ = posterior barbel. The vertical axis is an arbitrary scale relating to the gradations on the eyepiece graticule.

Barbus tongaensis Rendahl, 1935 *Annls Zool. Soc. Vanamo 2*(2): 14. The holotype (99PIS in the Department of Zoology, Turku University (Finland) was caught at Tonga (9°22′N, 31°06′E) in Sudan. This recent sample came from seasonal pools from between Jalle and Kongor, about 250 kms from the type locality. The size range of the sample is 18·5–25·00 mm SL and it contains sexually mature males and females, the latter are conspicuously deeper bodied than the males (see Fig. 25).

MORPHOMETRIC FEATURES. The morphometric features of a sample of 10 fishes covering the size range of the sample (including the holotype, 25 mm SL—in parentheses) are given below.
Body depth $\bar{x}$ = 30·9, range = 25·6–35·0; this very wide range reflects the depth of body of mature females (n = 4, range = 30·3–35·0); head length $\bar{x}$ = 28·6, range = 23·6–31·0 (26·8); eye diameter $\bar{x}$ = 8·5, range = 7·5–9·7 (8·0); interorbital width $\bar{x}$ = 10·8, range = 9·3–12·6 (12·0); pectoral fin length $\bar{x}$ = 19·6, range = 18·7–22·7 (19·6); caudal peduncle length $\bar{x}$ = 20·3, range = 18·6–23·0 (20·6); caudal peduncle depth $\bar{x}$ = 13·2, range = 12·1–14·6 (13·9); posterior barbel length $\bar{x}$ = 4·8, range = 3·6–6·1 (6·1) (only the posterior barbel is present); last unbranched dorsal fin ray length $\bar{x}$ = 26·7, range = 24·3–29·2 (broken in the holotype).

FINS. The dorsal fin has 3 unbranched (f10) and 7 (f2) or 8 (f8) branched rays. The anal fin has 3 unbranched and 5 branched rays (f10). The last unbranched dorsal fin ray is smooth, thin and flexible. All the fins are colourless.

SQUAMATION. The lateral line consists of only 3 (f3), 4 (f3), 5 (f3) or 6 (f1) perforated scales. The first one or two tubules lie within the mid-lateral pigment stripe but the rest follow a descending course below it.

The flank scales are deep (Fig. 26) and bear few radiating striae. The depth of the flank scales is reflected in the low number 8 (f10) of scales around the least circumference of the caudal peduncle.

Fig. 24 The holotype of *Barbus tongaensis*.

Fig. 25 *Barbus tongaensis*. Recently collected specimens to contrast the males (left) with the deeper bodied females.

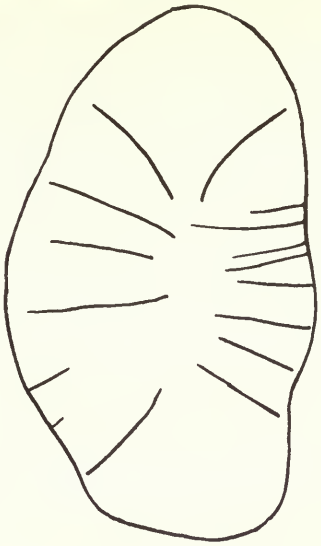

Fig. 26 A scale of *Barbus tongaensis*. Scale bar = 1 mm.

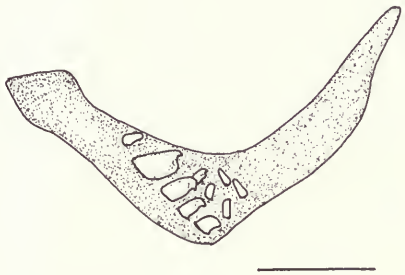

Fig. 27 A pharyngeal bone of *Barbus tongaensis*. Scale bar = 1 mm.

In the lateral line series there are 19 (f2), 20 (f4), 21 (f3) or 22 (f1) scales. Between the mid-dorsal line and the lateral line there are 4 (f10) scales and from there to the mid-ventral line there are 3 (f9) scales.

PHARYNGEAL TEETH. The pharyngeal teeth are arranged in three parallel rows of 2.3.5–5.3.2. (Fig. 27) and have hooked crowns.

GILL RAKERS. On the first ceratobranchial there are 5 (f4) or 6 (f5) short, dumpy gill rakers.

COLORATION. In alcohol preserved specimens the body colour is a pale yellow-brown. A dark narrow stripe runs from the top of the operculum to the end of the caudal peduncle. In smaller fish this mid-lateral stripe is expanded into a spot posteriorly. The stripe is not conspicuous in living fish (field observation by Dr R. G. Bailey). There is a faint brown median stripe in front of the dorsal fin. Only in smaller fishes is there a dark spot at the base of the anal fin.

Distribution of Nilotic *Barbus* species reaching a small adult size

The distribution of these *Barbus* species is interesting. Only one, *Barbus tongaensis,* is endemic, and is confined to the Sudd region of the White Nile. Of the remaining nine species, three, *B. kerstenii* Peters, 1868, *B. neumayeri* Fischer, 1884 and *B. pellegrini* Poll, 1939, occur within the Nile drainage only in the Lake Albert–Edward region but are otherwise variously widespread within East Africa. *Barbus pellegrini* extends as far as Lake Tanganyika, whilst *Barbus neumayeri,* the most extensively distributed of the three occurs widely over Uganda, Kenya and Tanzania. The distribution of this species and the other two is given in detail in Daget *et al.,* 1984. However, I am unable to trace the *Barbus neumayeri* locality of Lake Basuto that they cite, and suggest that it may be a misprint for Lake Basotu, a small lake at 4°22′S, 35°05′E on the Singida Plateau, Tanzania.

In contrast, the six other Nilotic species are at the eastern edge of their range. *Barbus anema* Boulenger, 1903 is found from the White Nile to the Chad and Niger basins. *Barbus leonensis*

Fig. 28 The first ceratobranchial of *Barbus tongaensis*. Scale bar = 1 mm.

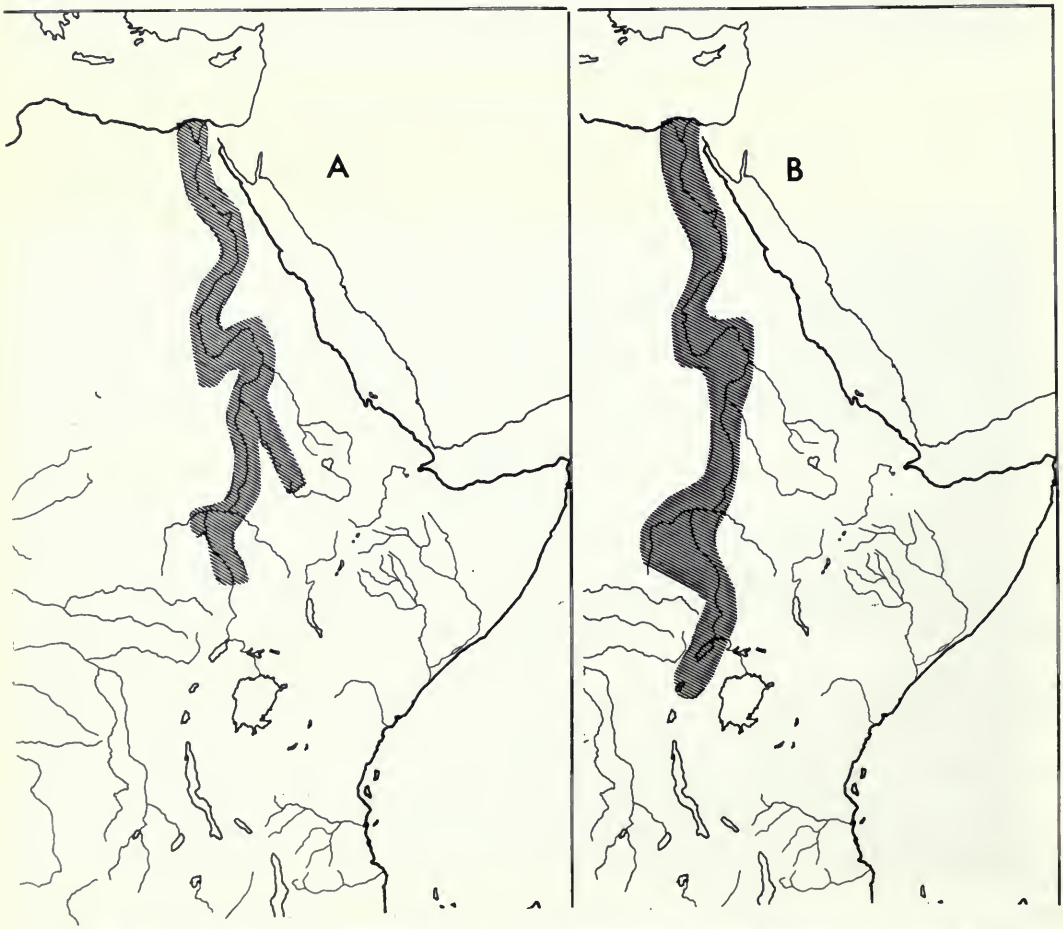

Fig. 29 The distribution within the Nile of (A) *Barbus perince,* (B) *Barbus stigmatopygus.*

Boulenger, 1915 occurs from the White Nile through the Chad, Niger and Volta systems to Gambia and Senegal. *Barbus perince* reportedly extends westwards as far as the Niger. *Barbus stigmatopygus* is found from the White Nile to the Volta. *Barbus yeiensis* Johnsen, 1926 and *B. pumilis* Boulenger, 1901 occur in the White Nile and Chad basins. Of these only the range of *Barbus perince* extends any distance up the Blue Nile (Fig. 29). The Blue Nile seemingly lacks small *Barbus* species except above the Tississiat Falls where there are species endemic to the Lake Tsana basin. However, in view of the inhospitability of much of the Blue Nile their absence is perhaps not surprising.

Barbus species, allegedly endemic to the Lake Victoria basin, do, however, occur in one Nilotic tributary. Greenwood (1963) noted the presence of the Nilotic species *Barbus perince* and *Barbus kerstenii* together with (*inter alia*) the Lake Victoria species *Barbus cercops* Whitehead, 1960 and *Barbus yongei* Whitehead, 1960 in the Aswa river, Uganda. The Aswa meets the Bahr-el-Jebel downstream of the Fola rapids and the town of Nimule in southern Sudan. Its headwaters are separated from the basins of Lakes Kyoga and Salisbury by a very low swampy divide. Greenwood (1963) suggested that the upper part of the Aswa river was formerly a part of the Victoria–Kyoga–Salisbury lake complex. Only a small tectonic movement would have been necessary to separate this arm of the lake and associate its drainage with that of the Nile. In view of the interesting faunal mixture in the Aswa river, it is unfortunate that the distribution of the various species within it is unknown.

Summary

(1) *Barbus neglectus* is a junior synonym of *Barbus perince*.
(2) *Barbus alberti* and *Barbus werneri* are both junior synonyms of *Barbus stigmatopygus*.
(3) When small (< *c.* 14 mm SL) *Barbus stigmatopygus* has no barbels and only the first few scales of the lateral line series have pores. At about 20 mm SL the lateral line is complete. Four characteristically long barbels are present in specimens over 30 mm SL.
(4) When adult (> *c.* 25 mm SL) *Barbus stigmatopygus* can be distinguished from spotted specimens of *Barbus perince* by the presence of a few large gill rakers confined to the upper part of the first ceratobranchial, and by the position of the middle spot which is on, or in front of, the vertical from the base of the last dorsal fin ray.

Key to the small *Barbus* species of the Nile (excluding Lakes Victoria and Tsana)

This key will only function when the fish have acquired most of their adult characters. Very small specimens are too similar to be keyed out. Delayed barbel development and lateral line tubule formation should be borne in mind.

1	Parallel striae on scales	Juvenile large *Barbus* species
	Radiating striae on scales	2
2	No barbels in fish > 16 mm SL	3
	Barbels in fish < 16 mm SL	5
3	Lateral line complete	*Barbus anema*
	Lateral line incomplete	4
4	Lateral line scales much deeper than long	*Barbus pumilis*
	Lateral line scales about as deep as long, dark spot on dorsal fin	*Barbus leonensis*
5	2 barbels in fish > 20 mm SL	*Barbus tongaesis*
	4 barbels in fish > 20 mm SL	6
6	First ceratobranchial with papillate tissue ventrally, few large gill rakers dorsally, flanks with up to 5 spots (NB juveniles have 0 or 2 barbels)	*Barbus stigmatopygus*
	No such papillate tissue, gill rakers ventrally on first ceratobranchial	7
7	Last unbranched dorsal fin ray smooth	8
	Last unbranched dorsal fin ray serrated	9
8	Body deep (> 30% SL at 35 mm SL), sometimes 3 spots on flanks, silvery	*Barbus perince*
	Body shallow (< 25% SL at 35 mm SL), irregular longitudinal stripe	*Barbus yeiensis*

9	No large spots or blotches on flanks	*.Barbus kerstenii**
	Large spots or blotches on flanks	10
10	Pelvic fin origin in advance of vertical from dorsal fin origin	*Barbus pellegrini**
	Pelvic fin origin more or less on the vertical from dorsal fin origin . . .	*Barbus neumayeri**

*within the Nile system limited to the Lakes Albert and Edward drainages.

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British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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The genera of pelmatochromine fishes (Teleostei, Cichlidae). A phylogenetic review

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Introduction

The main objectives of this paper are three-fold. First, to revise and review, at the generic level, a major group of west African taxa often referred to as the Pelmatochromines since all were once classified in the genus *Pelmatochromis*. Second, to determine whether these genera are closely related phylogenetically, and third, to examine their intrafamilial relationships. It is hoped that the information gained in this analysis will be a contribution towards any ultimate investigation of intrafamilial phylogeny in the Cichlidae as a whole.

The term 'pelmatochromine' used here has no implied or established taxonomic or phyletic implications. It is employed simply as a convenient reference to the various supraspecific groups recognised by Thys van den Audenaerde (1968*a*) in his revision of the speciose west African genus *Pelmatochromis* Steindachner, 1894.

Thys'[1] paper marks an important change in our taxonomic understanding of these fishes, especially since it is the first attempt to break down Regan's (1922) manifestly polyphyletic *Pelmatochromis* generic concept into a number of monophyletic lineages.

[1]Following current convention, Dr Thys van den Audenaerde's name will be abbreviated to Thys in all future references to his work cited in the body of the text.

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Although Thys retained his various lineages within a nominal *Pelmatochromis*, he did suggest the recognition of three subgenera (*Pelmatochromis, Chromidotilapia* Blgr. 1898, and *Pelvicachromis* Thys, 1968*a*). He also included, as a subgenus of *Pelmatochromis*, Pellegrin's (1904) *Nanochromis* which Regan (1922) had regarded as generically distinct from that genus but closely related to it. In addition to these four subgeneric groups, Thys included in *Pelmatochromis*, but as taxa *incertae sedis* with regard to their subgeneric placement, a number of species treated as members of *Pelmatochromis* by Regan (1922), together with others which had been described since 1922 (see Thys, 1968*a*, and pp. 154 & 160).

Later in the same year Thys (1968*b*) placed the nominate subgenus *Pelmatochromis* (*Pelmatochromis*) in *Tilapia* Smith, a move contested by Trewavas (1973) who resurrected the taxon as a genus, and thus by implication raised the other *Pelmatochromis* subgenera to full generic rank. Trewavas (*op.cit.*) also included in *Pelmatochromis* one of the species (*P. ocellifer* Blgr, 1899; but see Trewavas *op.cit.*) which Thys (1968*a*) had treated as being of uncertain subgeneric affinity, and resurrected another species (*P. nigrofasciatus* [Pellegrin, 1900]) which he had synonymised with *P. ocellifer* Blgr, 1899.

The following year Trewavas (1974) explicitly returned the subgenus *Chromidotilapia* to its former generic rank, thus, again by implication, recognising the subgenera *Pelvicachromis* and *Nanochromis* as genera.

Of the pelmatochromine taxa which Thys (1968*a*) treated as of uncertain infra-generic relationships, *Pelmatochromis ruweti* Poll & Thys (1965) has been placed in *Tilapia* (Thys, 1968*a*), *P. congicus* Blgr (1897) has become the monotypic taxon *Pterochromis* Trewavas (1973), *P. ansorgii* was made the type species of the genus *Thysia* Loiselle & Welcomme (1972), *P. cerasogaster* (Blgr, 1899) was included in *Hemichromis* Peters by Loiselle (1979), as was *P. exul* Trewavas (1933) by Trewavas (1973), and *P. thomasi* (Blgr, 1915) has become the type species of the currently monotypic genus *Anomalochromis* Greenwood (1985*b*).

Since *Pterochromis* and *Thysia* would, at least superficially, seem to qualify for inclusion in any review of the pelmatochromines, both are considered below. There seems no doubt that *Pelmatochromis ruweti* is indeed a species of *Tilapia* (see Trewavas, 1983), and that *Hemichromis* and *Anomalochromis* are not closely associated, phylogenetically, with the pelmatochromines (see Greenwood, 1985*a* & *b*; also p. 195). Thus, little more will be said about the two latter taxa except in a general context.

The pelmatochromines, as here restricted, are a moderately large group comprising some 35 species, to which more will undoubtedly be added when the various genera are subject to revisions at the species level. Geographically speaking, the assemblage is a west African one whose range extends from Senegal in the north to the Zaire river and several of its tributaries in the south. Within that area some of the constituent genera have relatively circumscribed distributions, and many of the species would appear to occupy even more localised areas. No pelmatochromines occur in any of the African Great Lakes (see below) and none has been recorded in other habitats within what is considered to be eastern Africa (i.e. east of longitude 29°E). Within west Africa no pelmatochromines have been recorded outside the region bounded by latitudes 18°N and 9°S. The supposedly unique pelmatochromine representative in east Africa, *Pelmatochromis exul* Trewavas from Lake Turkana, is now known to be based on the misidentification of three small *Hemichromis bimaculatus* specimens (Trewavas, 1973). In itself that corrected record is of interest since it represents the most easterly occurrence of *H. bimaculatus*, a species belonging to an otherwise essentially west African genus (see Loiselle, 1979; Greenwood, 1985*a*).

Most of the pelmatochromine species occupy fluviatile habitats, with some seemingly restricted to fast flowing, even torrential waters, as is the case with many *Nanochromis* species (see Roberts & Stewart, 1976; Stewart & Roberts, 1984).

In many respects the pelmatochromines are the ecological counterparts of several haplochromine taxa (*sensu* Greenwood, 1980) in east Africa, particularly with regard to species of the genera *Astatotilapia, Thoracochromis, Ctenochromis* and *Orthochromis* (Greenwood, 1979). It is this apparent haplochromine-pelmatochromine equivalence which, in part, aroused my interest in the pelmatochromines, particularly from the viewpoint of possible phyletic relationships between either individual genera or the two groups as a whole.

Thys' (1968*a*) analysis of the pelmatochromines was based on what are now called orthodox or evolutionary taxonomic lines. A cladistic (or Hennigian) approach is used here, both to test the hypothesis of intragroup relationships put forward by Thys (his subgenera) and to erect an hypothesis of interrelationships amongst those lineages, a problem only touched upon by Thys (1968*a*; fig. 17). Using the same methodology, I shall also attempt to establish the wider, intrafamilial relationships of these various lineages, especially to test Thys' (1968*b*) hypothesis that the phyletic relationship of at least some pelmatochromines lies with the genus *Tilapia* (*sensu* Trewavas, 1983).

Thys' inclusion of two *Pelmatochromis* (*Pelmatochromis*) species in *Tilapia* was strongly contested by Trewavas (1973), and I would support her views, albeit from a different standpoint. That difference raises questions about the validity, in phylogenetic arguments, of the characters used in previous discussions, and questions the current definition of the genus *Tilapia* itself and of the tilapiines *sensu* Trewavas (1983) as a whole, a lineage which includes certain pelmatochromine genera.

Materials and methods

Materials. The entire spirit collection of pelmatochromine species in the British Museum (Natural History) was examined. Those specimens from which new skeletal preparations were made are listed separately, together with those used for dissection; often a dissected specimen was later prepared as a skeleton.

Dissections used for previous studies (see Greenwood, 1978; 1983; 1985*a* & *b* and 1986), and named in those papers, are not detailed here.

Most of the British Museum (Natural History) collection of cichlid skeletal material (both dry and alizarin preparations) was examined or has recently been examined (see Greenwood, 1985*a* and 1986). For extra-familial out-group comparisons, the Museum's skeleton collections of the Serranidae, Centropomidae, Sparidae, Labridae and Pomacentridae was examined (see Greenwood, 1976; 1985*a*), and other anatomical data were derived from various specimens detailed in Greenwood (1985*a* & *b* and 1986).

All the specimens mentioned below are listed under the generic names in use before this revision, that is, following Thys (1968*a*) and Trewavas (1973 and 1974).

Additional material examined for superficial characteristics is as follows:

Museum of Comparative Zoology, Harvard University: *Nanochromis splendens*, holotype (MCZ 50476) and paratype (MCZ 50311); *N. parilius* holotype (MCZ 50474) and 8 paratypes (MCZ 50340); *N. consortius*, holotype (MCZ 50551); *N. minor*, paratype (MCZ 50310); *Pelmatochromis buettikoferi* (MCZ 35465, 60 & 38 mm SL); *Chromidotilapia guntheri* (MCZ 48071; *ca* 70 mm SL); *Chr.*cf. *guntheri* (MCZ 48135, *ca* 60 & 45 mm SL, and MCZ 32524, *ca* 70 mm SL). *Nanochromis longirostris* (MCZ 35398; 10 specimens 45–75 mm SL, and MCZ 35389, one specimen *ca* 60 mm SL). *Thysia ansorgii* (MCZ 48070, one specimen *ca* 54 mm SL).

Musée de l'Afrique Centrale, Tervuren: *Pelmatochromis nigrofasiatus* (det. E. Trewavas; registered as *P. ocellifer*), 3 specimens (from MCA 118090–99); *Pelmatochromis nigrofasciatus* 2 specimens (MCA 52454–55); *Nanochromis cavalliensis*, holotype (MCA 168574), and 4 paratypes (MCA 1963–471).

California Academy of Sciences: *Nanochromis robertsi*, holotype (SU 63143) and 2 paratypes (SU 67173).

British Museum (Natural History: *Myaka myaka* (1973.5.14:717–23). *Konia dikume* (1978.5.14:643–59); *K. eisentrauti* (1961.10.18:11–14). *Pungu maclareni* (1973.7.18:137–140). *Stomatepia mariae* (1973.5.14: 984–988); *S. mongo* (1971.10.20:24–33).

Dissections, partial dissections, and osteological preparations (see above) involved the following specimens (all from BM [NH] collections unless indicated otherwise): *Chromidotilapia batesii* (1912.6.29:4; skeleton), *Chr. finleyi* (1973.5.14:544; dissection and skeleton); *Chr. guntheri* (1973.5.14:615–625 and 1934.8.31: 179–188, one specimen of each: dissection and skeleton), *Chr. kingsleyae* (1867.5.3:2; 1912.4.1:526 and 1908.5.30:186; both skeletons). *Iranocichla hormuzensis* (paratypes, 1981.1.12:1–2; partial dissection of one). *Nanochromis cavalliensis* (holotype, MAC 168574; partial dissection of pharyngeal region); *N. parilius* (paratypes, MCZ 50475; 4 specimens as alizarin preparations, and BMNH 1977.1.11:33–34, paratype; one specimen as an alizarin preparation and partial dissection); *N. nudiceps* (1963.10.22:9, and one unregistered specimen, from below Stanley Pool, collected by Mr Owen Clark; both partial dissections). *Oreochromis macrochir* (J. L. B. Smith Institute, RUSI 22134; dissection); *O. mossambicus* (RUSI 19290; dissection); *O.*

niloticus (1981.2.17:601–620; one specimen partially dissected); *Pelmatochromis buettikoferi* (syntype, 1911.5.31:47; a skeleton, and 1981.6.19:103 and 1983.1.25:38; dissected and skeletonised); *P. longirostris* (1903.7.28:77–88; one specimen, an alizarin preparation, another dissected and skeletonised), *Pelvicachromis humilis* (1915.4.13:441; dissected and skeletonised, and 1972.3.16:8–10; one specimen dissected and skeletonised); *P. kribensis* (syntype, 1912.6.29:28; skeleton); *P. pulcher* (syntypes, 1901.1.28:13–20; one specimen dissected, and one already a skeleton; 1908.12.9:68; a skeleton); *P. subocellatus* (1888.12.13:8–10; one specimen skeletonised). *Thysia ansorgii* (1977.11.8:436–455; five specimens dissected and some skeletonised). *Tilapia busumana* (1934.8.31:189–199; one specimen skeletonised, and 1942.12.30:38–42; one specimen dissected and skeletonised); *T. ruweti* (1969.3.28:1–6; one specimen dissected and skeletonised; another specimen, ex Okavango Swamps, Botswana, unregistered, treated similarly); *T. sparrmanii* (1907.3.15:45–47; one specimen dissected and skeletonised, and RUSI 23538, dissected). *T. zillii* (1973.3.27:7–8; one specimen dissected). *Tristramella simonis* (1949.9.16:399–444; one specimen dissected and skeletonised).

A list of the *Tilapia, Oreochromis* and *Sarotherodon* species examined (and some partially dissected) in connection with the nature of the pharyngeal teeth and the arrangement of the pharyngeal bones (see pp. 148 & 198), and of the non-tilapiine taxa also examined is available in the Fish Section of this Museum.

Methods. The methodology employed has already been discussed in relation to that of Thys (1968*a*) and Trewavas (1973, 1974); no further comment is required (see p. 141 above).

Since the species-level taxonomy of the pelmatochromines, especially the genera *Pelvicachromis* and *Chromidotilapia*, is in a rather unsatisfactory state at present, I have concentrated my attentions on the type-species of the various genera. This is particularly so with regard to anatomical data and, where information is available, on the natural history of the species. Nevertheless, other species have not been neglected (where material permitted) and, as far as possible, are included when intergeneric comparisons are made. Likewise, particular attention has been paid to the correct specific identification of the specimens used. Whenever sample size allowed, these have been taken from amongst the syntypes of a species.

A review of Thys' supraspecific pelmatochromine taxa

As Thys (1968*a*) recognised, the pelmatochromines can be divided into two groups on the basis of at least one feature, namely the nature of the pharyngeal roof immediately anterior to the upper pharyngeal bones.

In one group, to which the majority of taxa belong, this tissue is organised into a distinct, visor-like pad projecting downwards and forwards for a short distance in front of and medial to the epibranchial of the first gill-arch, and is clearly circumscribed from the roof of the bucco-pharyngeal cavity by a distinct transverse groove (see Trewavas, 1974:389–391; Greenwood, 1983: 265–267). Associated with the presence of this pad (but probably not in a functional sense, see Trewavas, 1974; Greenwood, 1983) is an absence of microbranchiospines on any gill-arch.

The second group has no visor-like pad. The comparable area of the bucco-pharynx (as in the majority of cichlids) is merely a little more pachydermatous than the surrounding tissues. In this group, too, as in the majority of cichlids, microbranchiospines are present on the lateral aspects of gill-arches 2–4. The absence of a hanging pad, and the presence of microbranchiospines are taken to be the plesiomorphic condition in cichlids.

As was noted above (p. 140) Thys' supraspecific groups, some a little modified, are now recognised as genera, and some of his taxa, unallocated to a group, have recently been placed in newly described genera. It is as genera that they will be reviewed below.

I Pelmatochromines with microbranchiospines but without a pharyngeal hanging pad

PELMATOCHROMIS Steindachner, 1894

TYPE SPECIES: *Pelmatochromis buettikoferi* Steindachner, 1894 (subsequent designation by Regan, 1922:252).

SYNONYMY. *Pelmatochromis* (part): Steindachner, 1894 (the species *buettikoferi* only); Pellegrin, 1904 (the species *buettikoferi* [with which *ocellifer* was synonymised] and *nigrofasciatus*); Boulenger, 1915 & 1916 (the species *buettikoferi, ocellifer,* and *nigrofasciatus* [in part]); Regan, 1922 (the species *buettikoferi, corbali, nigrofasciatus* [in part], *longipinnis* [now a synonym of *nigrofasciatus*; see Trewavas, 1973]); Thys van den Audenaerde, 1968*a* (the species *buettikoferi, corbali* and *ocellifer*, with which *nigrofasciatus* was synonymised—but see Trewavas, 1973 for a correction of this misidentification); Trewavas, 1973 (the species *buettikoferi, nigrofasciatus* and *ocellifer*).

Paratilapia (in part): Boulenger, 1915 (the species *corbali* only).

Tilapia (in part): Thys van den Audenaerde, 1968*b* (the species *buettikoferi* and *ocellifer* (with which was included *nigrofasciatus*).

The *Pelmatochromis* generic concept has had a checkered history. Originally created by Steindachner for two species (one of which, *P. jentinki*, is now referred to *Tylochromis*; see Regan, 1922), the genus was expanded by Pellegrin (1904) to include 18 species. Boulenger (1915) continued this expansion by raising the number to 36. Regan's (1922) far more critical review of the 'generic' characters then recognised, reduced the number of species to 24. Thys' (1968*a*) review of Regan's *Pelmatochromis* concept actually increased the species number to 27. But, unlike previous revisors, he recognised the polyphyletic nature of the assemblage, breaking it down into a number of what he called 'natural groups' (Thys, 1968*a*:382). As an interim measure he designated those groups as subgenera.

The nominate subgenus in Thys' scheme contained but two species, *P. buettikoferi* and *P. corbali*, which, however, he thought were probably conspecific although he did not formally synonymise the two taxa.

The most recent revision (Trewavas, 1973) recognises three species (*P. buettikoferi, P. nigrofasciatus* and *P. ocellifer*, the latter being one of the species treated by Thys (1968*a*) as a *Pelmatochromis* of uncertain subgeneric affinity, but which he later [1968*b*] transferred, with the other two, to *Tilapia*). Trewavas (*op.cit.*) makes no reference to *P. corbali*, presumably accepting Thys' (1968*a*) view that it is a synonym of *P. buettikoferi.*

One reason for this conceptual instability, at least when seen in retrospect, would seem to be the persistent lack of any critical definition for the genus. That is to say, a definition based on derived characters uniquely shared by all the constituent species. In every definition to date, the characters used are either plesiomorphic ones or, if apparently derived ones (like the unicuspid jaw teeth and cycloid scales), are widely distributed amongst other taxa. Those other taxa, however, are each definable on the basis of their own and uniquely shared synapomorphies, suggesting that the apomorphies shared with *Pelmatochromis* are either homoplasies or features indicative of relationship at a very distant level. In other words, *Pelmatochromis* is, and always has been defined and categorised on the absence rather than the presence of defining features, a sort of monophyly by default. Its real monophyly has yet to be established.

Thys (1968*a*) defined the subgenus *Pelmatochromis (Pelmatochromis*) on the basis of its members possessing microbranchiospines (absent in members of all his other named *Pelmatochromis* subgenera, but present in one of his unnamed groups) and not having a *Tilapia*-spot, but instead a dark blotch (the so-called *Pelmatochromis*-spot) on the flank immediately below the soft dorsal fin.

The presence of microbranchiospines cannot be considered a derived feature within the Cichlidae (see Stiassny, 1981). The absence of a *Tilapia*-spot might, on the other hand, seem to be an apomorphy since its presence is apparently a plesiomorphy amongst African cichlids (Oliver, 1984; personal observations). Furthermore, it would seem that a *Pelmatochromis*-spot could be interpreted as a derived condition of the plesiomorphic *Tilapia*-spot. However, a *Tilapia*-spot is present in two of the three *Pelmatochromis* species (see Trewavas, 1973:12), and in one of these (*P. nigrofasciatus*) it sometimes occurs in combination with an incipient *Pelmatochromis*-spot (*op.cit.*: 7). On the basis of those data, the presence or absence of a *Tilapia*-spot and, or, the presence of a *Pelmatochromis*-spot would be of doubtful value for establishing the monophyly of what is now the genus *Pelmatochromis.*

Three other seemingly derived features of *Pelmatochromis* (cycloid scales, unicuspid jaw teeth, and the shape of the gill-rakers) must also be considered.

On the basis of outgroup comparisons amongst perciform fishes, ctenoid rather than cycloid

Fig. 1 Anterior premaxillary teeth (frontal view) of *Pelmatochromis buettikoferi*. Magnification ×16 (BMNH 1911.5.31:47).

scales should be considered plesiomorphic. The situation within the Cichlidae is, in my view, less readily interpreted (see discussions in Greenwood, 1979, and Oliver, 1984). If, as Oliver (1984) argues, cycloid scales are to be treated as apomorphic (i.e. derived) features in the Cichlidae, then I would agree with his further suggestion that they '... arose two or more times in the family'. The value of cycloid scales for establishing the monophyly of *Pelmatochromis* can, however, be discounted since the scales in all pelmatochromine taxa are predominantly of that type.

Large specimens of all three *Pelmatochromis* species have, in the outer row of both jaws, teeth which are relatively slender unicuspids, their crowns somewhat attenuated and slightly compressed (Fig. 1). Such unicuspid teeth can, in my opinion, be considered an apomorphic feature within the cichlids, even though unicuspids occur commonly amongst percoid outgroups. My argument for considering unicuspid teeth in cichlids as a derived feature is as follows:

i. Unicuspid teeth in such basal percoids as the Serranidae and Centropomidae are small, very numerous and form a relatively dense felt on the alveolar surface of the dentigerous jaw bones, with no clear differentiation between outer and inner tooth rows. In cichlids with unicuspid teeth, those in the outer row are clearly larger than the inner row teeth, are usually separated from the latter by a distinct gap, are well separated from one another and, relative to the basal percoid type, are larger.

ii. Whenever it has been possible to study the post-larval ontogeny of jaw teeth in cichlids, a definitive unicuspid dentition in the outer tooth rows is preceded by one of essentially bicuspid or weakly bicuspid teeth in which the minor cusp forms a sort of shoulder to the major cusp (Greenwood, 1974; 1982). Such early bicuspids may be interpreted as an interim dentition since, in the few examples studied, the earliest recognisable jaw teeth present in buccal larvae are very fine, needle-like objects (see Greenwood, 1956:228 for haplochromines; Fishelson, 1966:596–7 and fig. 28 for *Tilapia tholloni* where the teeth are described as tricuspidate but the photograph indicates otherwise; and Balon, 1977:165 for *Labeotropheus* species).

The occurrence of some bicuspid teeth in *P. nigrofasciatus* was noted by Thys (1968*a*:370; fig. 16), but at that time this species was misidentified as *P. ocellifer* (see Trewavas, 1973) and was thus not included in his subgenus *Pelmatochromis* (*Pelmatochromis*). These bicuspid teeth are discussed in detail by Trewavas (1973:6; fig. 4) who showed that distinctly bicuspid (i.e. 'notched') teeth in *P. nigrofasciatus* are found only in small fishes, and are less numerous than the slender conical ones

with which they occur. The sole specimen with notched teeth available to Trewavas is 22 mm SL; in the next larger specimen she examined (38 mm SL) notched teeth are absent and are replaced either by unicuspids or by very weakly bicuspid teeth in which the minor cusp is reduced to no more than a shoulder continuing the base of the major cusp towards the margin of the tooth (*op.cit.*, fig. 4). Such shouldered teeth, unlike the unicuspids which replace them, have flattened and not conical crowns.

I have re-examined the small *P. nigrofasciatus* studied by Trewavas and can confirm her observations. Furthermore, I find that in two larger individuals (100 and 109 mm SL, MRAC 52454–5 identified by Trewavas) some outer teeth situated posterolaterally in the dentary have faint indications of a shoulder and, like definitely shouldered teeth, have an obliquely cuspidate and compressed, not conical, major cusp. Similar shadow-shouldered teeth occur in a 65 mm SL specimen (from MRAC lot number 118090–99), which also has some more obviously bicuspid (i.e. notched) teeth amongst the unicuspids. In both these specimens the non-unicuspid teeth are not restricted to any particular region of the jaw.

Shadow-shouldered teeth, identical with those in *P. nigrofasciatus*, occur amongst the slender, conical-crowned unicuspids in the outer tooth rows of both jaws in the holotype of *P. ocellifer*, a specimen of *ca.* 65 mm SL. Many teeth are missing from this now poorly preserved specimen but it seems likely that the shadow-shouldered forms were confined to the anterior and anterolateral regions of the jaws.

Thus, *pace* Trewavas (1973:14) it seems that barely recurved, weakly shouldered teeth, quite unlike the definitive conical-cusped and moderately recurved unicuspids, occur in small specimens of at least two *Pelmatochromis* species, and that some may persist in larger individuals. Trewavas, on the contrary, believed that in *P. buettikoferi* and *P. ocellifer* the '. . . outer teeth are curved and conical at all stages from a standard length of 28 mm'.

Teeth in the inner rows, at least in *P. nigrofasciatus* (Trewavas, 1973:12) also undergo an ontogenetic change in form, being unicuspid in fishes of 68 mm SL and above, but shouldered in smaller individuals. However, the inner teeth in the smallest *P. ocellifer* and *P. buettikoferi* examined are all small and slender unicuspids.

The ontogenetic changes leading to a unicuspid adult dentition in the jaws of two *Pelmatochromis* species would seem to reinforce the assumption that the definitive dentition in this taxon represents a derived condition. A unicuspid definitive dentition, of course, occurs in many cichlid genera (including other pelmatochromines), taxa which, in most cases, can be defined on the basis of their own autapomorphic features, or which have other apomorphic characters not present in *Pelmatochromis*. Thus, in itself the unicuspid dentition of *Pelmatochromis* could as well be a synapomorphic character indicative of that taxon's membership in some larger phyletic assemblage, rather than an autapomorphy for the genus alone. Without the support of other congruent autapomorphies it does not establish the monophyly of the genus.

The third apparently derived feature shown by *Pelmatochromis* concerns the morphology of the gill-rakers (Fig. 11). Although there is a very wide range of gill-raker form, size and arrangement in African and in Neotropical cichlids, the rakers in the outer row on the first gill-arch in all three *Pelmatochromis* species are of a type rarely encountered in the family. They are also quite unlike those found amongst other members of the Labroidei (the suborder to which the cichlids belong) or in the majority of percoid fishes. On those grounds I would consider that the rakers in *Pelmatochromis* are indeed apomorphic. But again, there is the problem of whether or not the character is an autapomorphic one, and thus indicative of the taxon's monophyly (see below).

The outer ceratobranchial gill-rakers in *Pelmatochromis* are moderately long, pachydermatous structures, so arranged on the greater part of the arch as to be directed obliquely forward across its surface and not, as is the usual condition, pointed aborally away from the arch. In outline each raker is approximately crescentic (the concave face uppermost), deep over most of its length but with the distal part drawn out rather abruptly into a fine, bluntly pointed, horn-like tip. Proximally at least, the membrane covering the bony skeleton of the raker is continued medially where it meets a prominent ridge of tissue running a little mediad to the midline of the arch. Between each of the rakers of the inner and outer rows this ridge is drawn-up into a prominent but low papilla. Over the concave upper surface of each raker (but most noticeably in those on the middle section of each

arch) its covering tissue is thrown into numerous, contiguous, low tubercles, so that the raker comes to resemble the chela of a crab's claw (albeit a rather compressed one).

The inner rakers of this arch are shorter than their outer counterparts, and are subconical in shape; as in the outer rakers, the aboral surface is tuberculate. Inner and outer row rakers are virtually continuous, the gap between them being filled by the low papilla noted above.

There is apparently some interspecific variation in the morphology of the outer rakers on the first arch, both in the extent to which the distal 'horn' is produced (and thus is more or less obvious and horn-like) and in the degree to which the aboral face is tuberculated. Since, however, these features are formed in soft tissue it is possible that both could be influenced by fixation and preservation, by the time for which the specimen has been preserved, and by prefixation *post-mortem* changes.

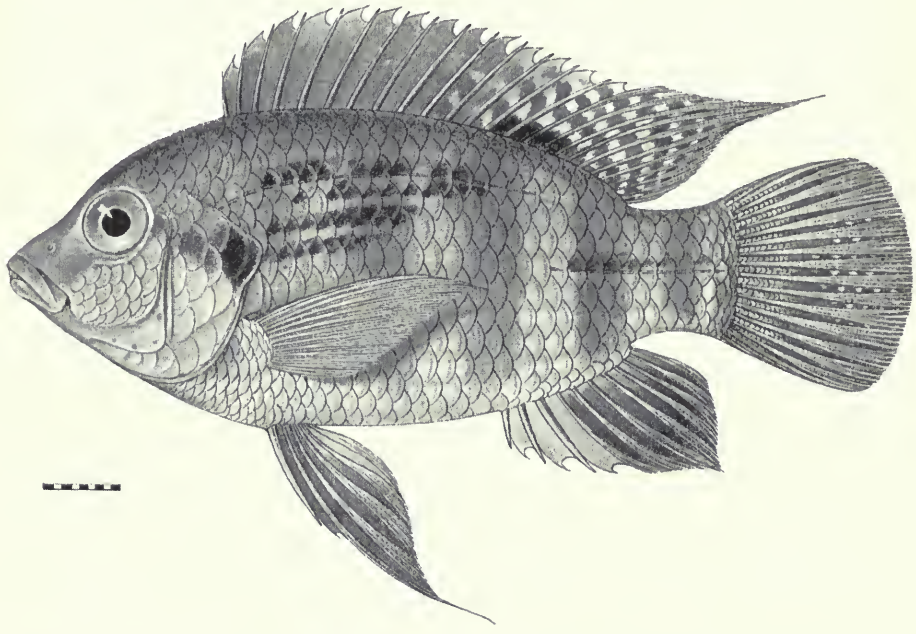

Fig. 2 *Pelmatochromis ocellifer*; from the original drawing by J. Green. Scale bar in mms.

Both rows of gill-rakers on the epibranchial part of the first arch are simple, slender and relatively long, and are implanted at right angles to the arch's surface.

Although the ceratobranchial gill-rakers in *Pelmatochromis* can be ranked as an apomorphic feature, it is difficult to decide whether they should be considered an autapomorphy for the genus rather than a synapomorphy shared with most other pelmatochromine taxa except *Pterochromis* (for which see p. 155).

Allowing for possible influences of preservation and other chance factors, gill-raker morphology in these other taxa seems merely to be an intensification of certain details (tuberculation, thicker epithelial cover, and greater attenuation of the horn-like tip) found in *Pelmatochromis*. On the present evidence I would withold a final judgement on that point, but would note here that the evidence suggests synapomorphy rather than autapomorphy (see p. 191).

Since none of the three presumed apomorphic features of *Pelmatochromis* can be established unequivocally as an autapomorphy, the monophyly of the genus still cannot be established. Its status as a discrete taxon is based only on its possessing a suite of characters, both apo- and plesiomorphic which, taken in combination, differentiate it from other superficially similar taxa.

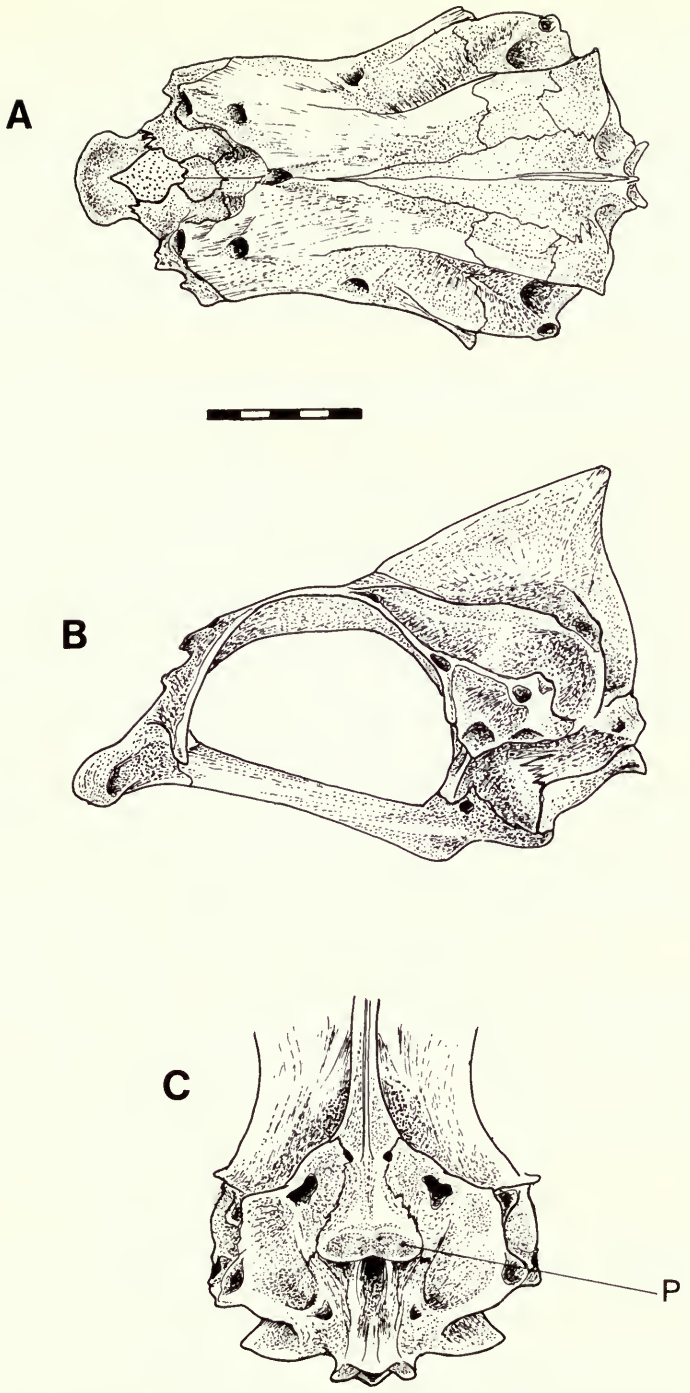

Fig. 3 *Pelmatochromis buettikoferi*. Neurocranium in: A. Dorsal; B. Left lateral view. C. Neurocranial apophysis for the upper pharyngeal bones. P = parasphenoid. Scale bar in mms (BMNH 1911.5.3:48).

Interestingly, Trewavas (1973:19) commented that '. . . the adult dentition of *P. nigrofasciatus* is itself so distinct as to suggest that *Pelmatochromis* is diphyletic', but did not develop her argument further nor, in that particular context, did she indicate the nature of the distinction. Presumably she is referring to the size discrepancy between inner and outer row teeth in this species as compared with the condition in other *Pelmatochromis* species, and to the slight posterior broadening of the inner tooth rows of the dentary. In the absence of any other seemingly autapomorphic morphological features in *P. nigrofasciatus* (its reproductive isolation is assumed), or derived features shared uniquely by the two other species, the possibility of the genus being non-monophyletic can no more be established than can its monophyly.

The interrelationships of *Pelmatochromis* are discussed on p. 192 below.

DIAGNOSIS. Several of the features noted here are discussed in more detail on pp. 149–153. *Pelmatochromis* is distinguished from other genera of African cichlids by the following characters taken in combination:

Body moderately deep (Fig. 2), not fusiform.

Neurocranial apophysis for the upper pharyngeal bones formed from the parasphenoid alone

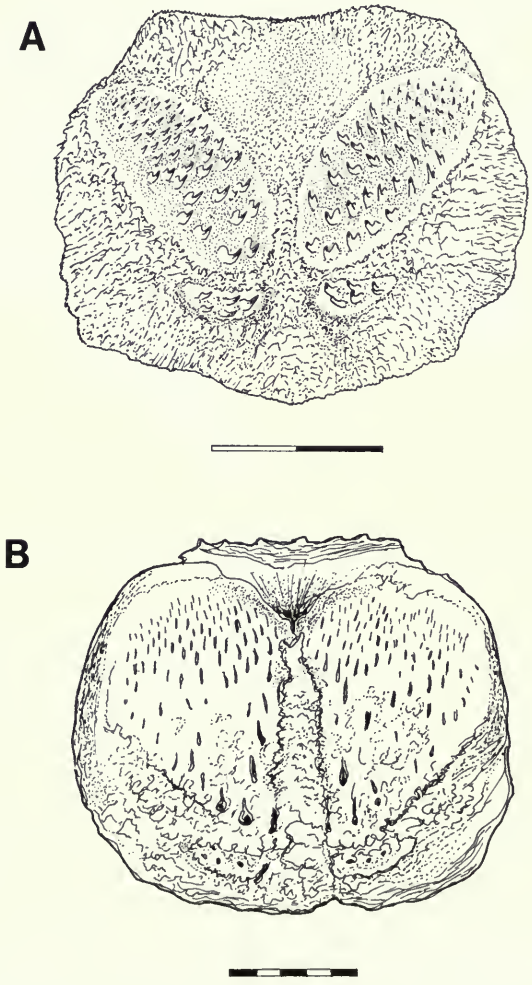

Fig. 4 Occlusal view of the upper pharyngeal bones, *in situ*, of: A. *Parananochromis longirostris* (BMNH 1903.7.28:77–83), and B. *Tilapia zillii* (BMNH 1973.3.27:7–8). Scale bar in mms.

(i.e. of the *Tilapia*-type; Fig. 3C); supraoccipital crest prominent (Fig. 3B); supraethmoid not contacting the vomer (at least in *P. buettikoferi*).

Palatine with a two-point neurocranial contact, anteriorly through an articulation in the region of the ethmovomerine suture, and posteriorly with a facet on the ventral face of the lateral ethmoid (see Greenwood, 1985*a*); a calyx present between the metapterygoid and the hyomandibula (see Greenwood, 1985*a*; 1986).

Prepharyngeal pad in the bucco-pharyngeal roof prominent but not developed into a visor-like hanging pad clearly demarcated from the surrounding tissue. Posterior facing margins of the major upper pharyngeal bones (the fused pharyngobranchials 3 and 4) so aligned as to form a broad and shallow V whose apex is directed anteriorly (see Fig. 4A). No 'kukri'-shaped teeth on the lower pharyngeal bone (see p. 197 and Fig. 30), the teeth of which all have the tip of the major cusp pointing forwards and lying a little anterior to, or in the same vertical as the tooth's posterior margin. Anterior blade of the lower pharyngeal bone short, its length contained 3–4 times in the overall length of the bone.

Infraorbital bones forming a complete lower and posterior margin to the orbit, the first infraorbital (lachrymal) longer than deep and with 4 openings to its laterosensory canal (Fig. 5A).

Outer row jaw dentition, at least in fishes >25 mm SL, composed predominantly of slender and slightly recurved unicuspids with attenuated conical crowns (Fig. 1); in smaller specimens some weakly cuspidate teeth with notched or shouldered crowns also occur (see p. 144); inner tooth rows are composed mainly of slender unicuspids.

Ascending process of the premaxilla 30–35 percent of head length. Anguloarticular with roofed canal for the mandibulo-preopercular laterosensory canal. Lower jaw length less than half head length.

Scales cycloid, 25–30 pored scales in the lateral-line series; upper lateral-line clearly separated from the dorsal fin base over the line's entire length, and by at least $2\frac{1}{2}$ or 3 scales at its highest point (*ca* the 8th scale in the series), and by $1\frac{1}{2}$ or 2 scales over the last pored scale; 16 scales around the caudal peduncle. Cheek with 3 scale rows. Chest scales not noticeably smaller than those situated anteriorly on the ventral and ventrolateral aspects of the flanks and belly.

Gill-rakers in the outer row on the ceratobranchial of the first gill-arch number 14–16, are transversely orientated across and close to the arch, are long, pachydermatous and crescentic, have the concave upper surface tuberculate, and the distal tip produced and horn-like. These rakers are continuous with a prominent projection developed from the membranous ridge extending down the middle of the gill-arch (see p. 145). Gill-rakers on the epibranchial of the first arch number 3–8, are simple, relatively slender and elongate, and are arranged in two rows.

Microbranchiospines present on the outer face of gill-arches 2–4.

Modal total number of vertebrae 25; there are 13–15 (mode 14) abdominal and 10–12 (mode 11) caudal vertebrae (all counts exclude the fused PU1 and U1 centra). Spondylophysial apophysis for the retractor pharyngeal muscles well-developed and situated on the 3rd centrum.

A single supraneural (predorsal) bone. Dorsal fin with 13–15 spines, anal fin with 3 spines.

Tilapia-spot present in at least the young of two species, 'replaced' ontogenetically in one of those species by a *Pelmatochromis*-spot which is also present in a third species that never develops a *Tilapia*-spot (see Trewavas, 1973 and p. 143 above).

All species are substrate guarders.

NOTES ON THE ANATOMY AND OTHER FEATURES. Anatomical and osteological studies have been made principally on the type species, *P. buettikoferi*, but certain osteological features were checked from radiographs and by superficial dissections of *P. ocellifer* and *P. nigrofasciatus*.

In most features the cranial and pharyngobranchial myology, osteology and arthrology of *P. buettikoferi* depart but slightly, if at all, from what seemingly can be taken as the modal and plesiomorphic condition for African cichlids. In an intrafamilial context there are few derived features (see Barel *et al.*, 1976; Cichocki, 1976; Anker, 1978; Stiassny, 1981*a* & 1982; Greenwood, 1983 & 1985*a*).

Osteology. The *neurocranium* (Fig. 3) has the plesiomorphic *Tilapia* type of apophysis for the upper pharyngeal bones (Greenwood, 1978) in which the entire articular surface is contributed by the

parasphenoid. The skull (Fig. 3) is relatively foreshortened and broad interorbitally, and the ethmovomerine region is somewhat decurved, sloping downwards at an angle of *ca.* 50° to the horizontal.

The ethmovomerine length (measured directly from the anterior tip of the vomer to the lateral tip of the lateral ethmoid) is short and is contained about $3\frac{1}{4}$ times in the neurocranial length (measured directly from the anterior tip of the vomer to the ventral rim of the basioccipital facet). At least in *P. buettikoferi* (the other species could not be examined) the supraethmoid does not contact the vomer, an unusual feature (see Trewavas, 1973; Greenwood, 1985*a*) but one of as yet indeterminable phylogenetic significance.

In *P. buettikoferi* (again the only species which could be checked) the lateral commissure of the *pars jugularis* is of the *Haplochromis*-type, and there is a stout precommissural bridge between the

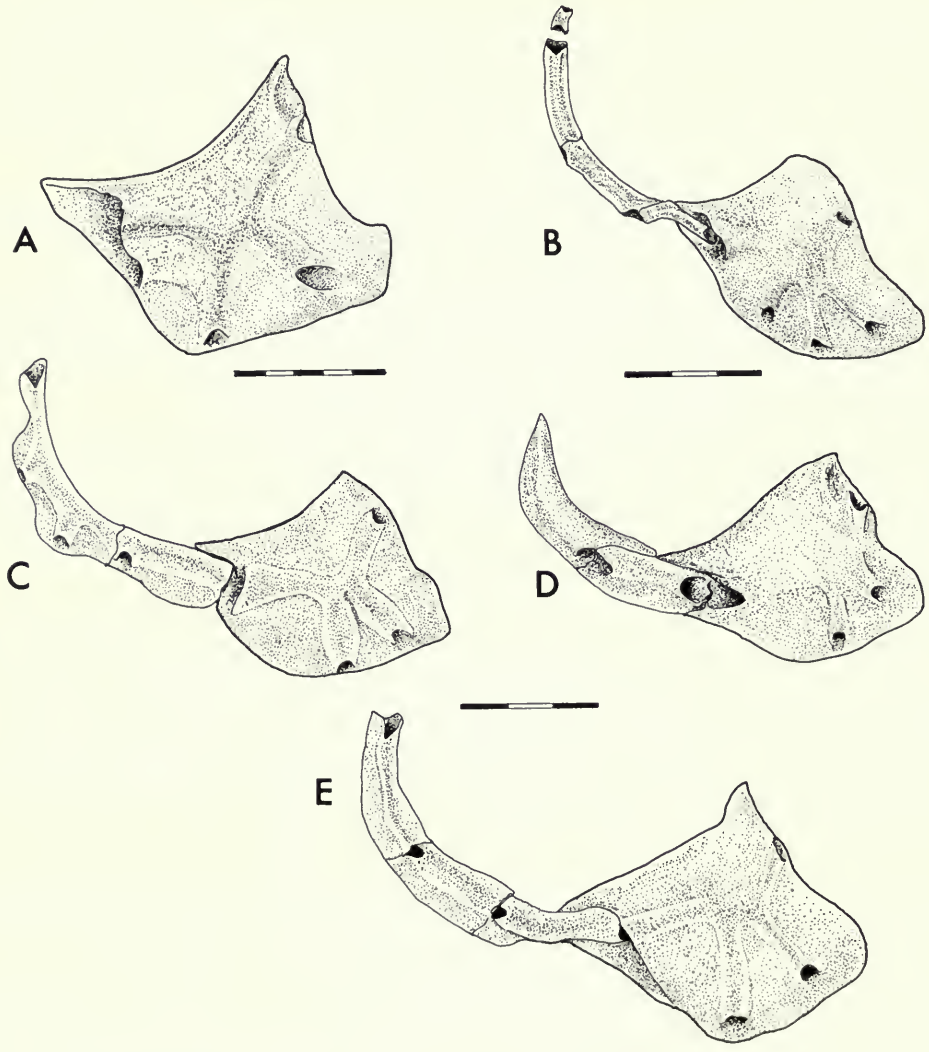

Fig. 5 Right infraorbital bones of: A. *Pelmatochromis buettikoferi* (lachrymal only); B. *Chromidotilapia guntheri* (lachrymal+4 others); C. *Parananochromis longirostris* (lachrymal+2 others); D. *Pelvicachromis pulcher* (lachrymal+2 others); E. *Thysia ansorgii* (lachrymal+2 others). Scale bar in mms.

prootic and pterosphenoid bones (see Greenwood, 1986). An *Haplochromis*-type lateral commissure is a plesiomorphic feature, but the significance of a precommissural bridge is still unknown (Greenwood, *op.cit.*).

The supraoccipital crest is well-developed and relatively long basally, its anterior point lying above about the mid-point of the orbit.

The *infraorbital bone series* (Fig. 5A) is complete, with almost half the second ossicle overlapping a posterior, plate-like flange developed below and behind the posterior lateral-line canal opening of the lachrymal. There are four lateral-line canal openings in the lachrymal, the presumed plesimorphic condition in cichlids (Trewavas, 1983; Greenwood, 1985*a*).

Few characters associated with the *pharyngobranchial skeleton* in *P. buettikoferi* require comment. There is a very broad and elongate, near-rectangular cartilaginous expansion of the second epibranchial's anterior margin (see fig. 11 in Trewavas, 1973). This process is partly lodged within the body of the prepharyngeal pad. From my own observations on a number of African cichlids there is apparently little or no correlation between the extent to which the cartilage is developed and the degree to which the pad is developed, unless it is of the hanging pad type. For instance, in both *Orthochromis machadoi* and *Hemichromis bimaculatus* the prepharyngeal pad is very well-developed and approaches the visor-like hanging pad found in several pelmatochromine taxa (but not *Pelmatochromis*). Yet, in *O. machadoi* and *H. bimaculatus* the cartilage is very poorly developed (Greenwood, 1984*a* & 1985*a*). It seems, however, that in species with a fully-developed hanging pad the cartilage is always extensive (personal observations on various pelmatochromine species, and in those members of the *Ophthalmotilapia* assemblage from Lake Tanganyika which have a hanging pad; see Greenwood, 1983). Unfortunately, this cartilage is invariably shrivelled in dry skeletons, and to date few alcian-blue counterstained alizarin preparations are available for study. Thus the validity and significance of my few observations cannot be tested. It should be noted that in the *Tilapia busumana* dissected for this purpose, the cartilage is as extensive as that in the *Pelmatochromis nigrofasciatus* illustrated in fig. 11 of Trewavas (1973), and does not resemble the smaller and very differently shaped cartilage that author shows for *T. busumana*. It is difficult to tell, however, whether these differences are attributable to intraspecific variability or to the techniques used for preparing the specimens.

The quadrangular area of epibranchial 4 in *P. buettikoferi* is deep and near-rectangular, and the shank spine is ridge-like; the bone thus closely resembles that of *Chromidotilapia kingsleyae* illustrated by Greenwood (1985*a*; fig. 15B).

The *lower pharyngeal bone* in all species (Fig. 6A; and figs 5A–D in Trewavas, 1973) has a short anterior blade (*ca.* $3\frac{1}{2}$–4 times in the overall length of the bone, measured as the vertical between the tip of the blade and the tips of the articular horns). Its posterior margin has a deep median indentation so that the outline of the bone is distinctly arrow-head shaped. There are some, slight, interspecific differences in the lower pharyngeal dentition (see Trewavas, 1973), but no major modifications are apparent in tooth shape or cusp form, which are essentially of the generalised African cichlid type (see p. 197 for a description and discussion of the 'kukri'-shaped teeth in tilapiines). The upper pharyngeal teeth are likewise of a generalised type. The *upper pharyngeal bones* (pharyngobranchials 2 and 3+4, the former lying anterior and closely apposed to the latter) are so arranged that the posterior facing medial margins of the fused third and fourth pharyngobranchials of each side form a broad and shallow V. The apex of the V, the second pharyngobranchials, is directed anteriorly (Fig. 4A). In outline the fused third and fourth pharyngobranchials are narrowly sub-ovoid. A broadly V-shaped arrangement of the upper pharyngeal bones is the plesiomorphic condition for both the African and Neotropical cichlids (see discussion on p. 198).

Little comment is required on the *caudal fin and axial skeleton*, except to note that the single supraneural bone is well-developed, that there is (at least in *P. buettikoferi*) a stout and prominent spondylophysial apophysis on the third centrum, and that the number of vertebrae is low, both in total and in separate counts of abdominal and caudal elements. Again, this is the plesiomorphic condition. In all three species there are 13–15 (mode 14) abdominal vertebrae and 10–12 (mode 11) caudal elements, giving total counts of 24–26 (mode 25); the fused PU1 and U1 centra are not included so that the total is lower than that given by Trewavas (1973).

No outstanding features were noted in the skeleton of the *jaws*, or in the *suspensorium and palatoquadrate arch*.

A distinct calyx formed from the metapterygoid and hyomandibula, and open medially, is present (see Greenwood, 1985*a*), and the mandibulo-preopercular laterosensory canal passes through a roofed canal in the anguloarticular bone (see Greenwood, 1985*a* & *b*). There are five

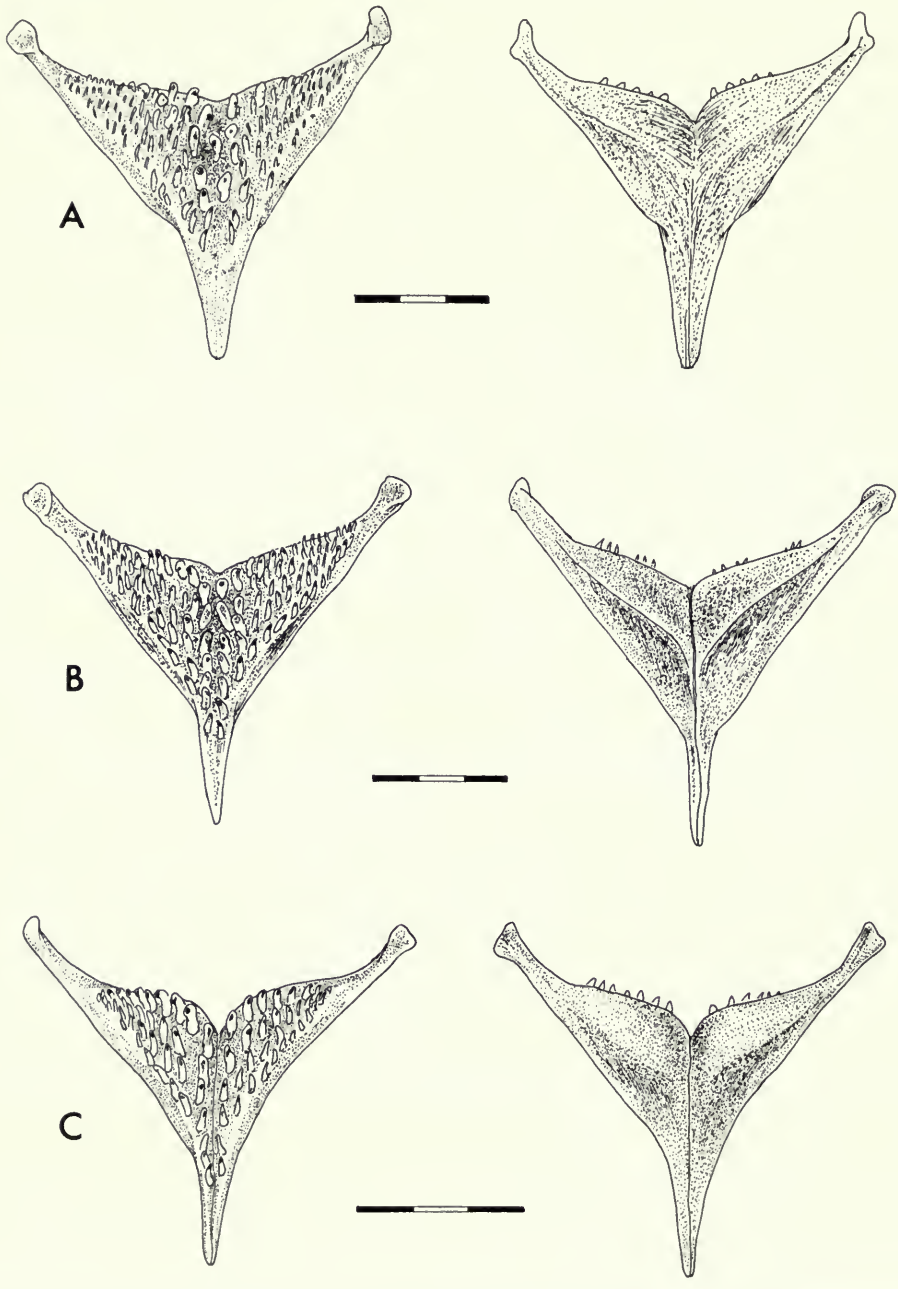

Fig. 6 Lower pharyngeal bone, in occlusal (left) and ventral (right) views, of: A. *Pelmatochromis buettikoferi*; B. *Thysia ansorgii*; C. *Chromidotilapia finleyi*. Scale bar in mms.

laterosensory openings in the dentary and seven in the preoperculum; that is, the usual number amongst African cichlids and in the majority of Neotropical taxa as well. Both these conditions are plesiomorphic for cichlids, but the calyx is a widespread apomorphy in the family.

Squamation. The scales in all *Pelmatochromis* species are predominantly cycloid ones, with a few weakly granular scales sometimes occurring as well. Scales on the chest are not noticeably smaller than those on the belly and ventrolateral aspects of the flanks, and what size change there is takes place gradually. The cheek is completely scaled, being covered by three rows at its deepest point. The upper lateral-line is, at its highest point, separated by at least $2\frac{1}{2}$ scale-rows from the dorsal fin base, and there are at least $2\frac{1}{2}$ scale-rows above the last pored scale in the series. There are 16 scales around the caudal peduncle, the commonest and probably plesiomorphic condition in African cichlids.

Fins. No sexual dimorphism is apparent in the shape of the caudal fin, which has a gently rounded margin. Neither is there a marked dimorphism in pelvic fin shape. Here the first unbranched ray is clearly the longest in both sexes although, relatively, that ray may be longer in males than females; however, the small sample sizes available for all species, and the difficulty of sexing many of the specimens, require that observation to be checked.

Other external features and the *dentition* are discussed on pp. 143–145.

Myology and arthrology of the jaws and palatoquadrate arch. No really outstanding features were noted in either system of *P. buettikoferi*; both closely approximate to the generalised condition amongst African cichlids (see Anker, 1978; Stiassny, 1981*a* & *b*, & 1982; Greenwood, 1985*a*).

Tendon A1β of the *adductor mandibulae* I muscle is very broad, and fuses completely with the tendon of adductor muscle Aw (i.e. like the condition in *Hemichromis* but unlike that of the other taxa examined; see Stiassny, 1981*a* & *b*; Greenwood, 1985*a* and unpublished observations). As in *Hemichromis* a discrete division of A1β tendon inserts on the nipple process of the anguloarticular.

Muscle A3 of the *adductor mandibulae* complex is poorly developed, its anterior half being entirely tendinous. The *adductor arcus palatini* muscle has an extensive insertion on the palatine bone (see Greenwood, 1985*a*; 169).

The *dorsal gill-arch muscles* of *P. buettikoferi*, like the musculature of the jaws and palatoquadrate arch, are essentially similar to those of other generalised cichlids. They closely resemble *Hemichromis* (Greenwood, 1985*a*) in their general lay-out, although the relative size of certain muscles is different. The major association of the *levator externus* 4 with the horn of the lower pharyngeal bone is exactly as in *Hemichromis*. Also as in *Hemichromis*, only a small slip of the *levator posterior* muscle inserts on the horn, the major part of the muscle being inserted on the fourth epibranchial bone (see Greenwood, 1985*a*:159–162).

Muscles derived from the circumoesophageal series, and extending forward between the upper pharyngeal bones to insert on the 2nd and 3rd pharyngobranchials (Anker's [1978] 'sub-epithelium muscular tissue'), are well-developed. They originate as a single longitudinal band which bifurcates anteriorly at a point about two-thirds of the way along the length of the third pharyngobranchial.

Ventral gill-arch musculature. The *rectus ventralis* and the *obliquus ventralis* muscles have the same relationship with the semicircular ligament as do the muscles in *Hemichromis* and a number of other African and Neotropical species I have dissected (see Greenwood, 1985*a*; also unpublished observations, and p. 163 below).

The *transversus ventralis anterior* muscle is interrupted medially by the anterior blade of the lower pharyngeal bone, the common condition in African taxa (see Stiassny, 1982:442; fig. 13(a)).

Relationships. The virtual absence of unequivocally autapomorphic features amongst the characters studied makes it impossible to corroborate the assumed monophyly of *Pelmatochromis* (see p. 146 above). Likewise, the absence, except for one possible character, of synapomorphic features with a relatively restricted distribution amongst other cichlids, makes it impossible to hypothesise, with moderate certainty, a sister-group for the genus, or to suggest that its contained taxa be transferred to some other genus or genera. Certainly there is no evidence to support Thys' (1968*b*) idea of placing two species in the genus *Tilapia* (see also Trewavas, 1973), a problem discussed further on p. 195.

The single derived and possibly synapomorphic feature noted above is the morphology of the gill-rakers. It would certainly argue against a relationship with *Tilapia*, but does suggest

Pelmatochromis could be the plesiomorphic sister taxon to all the other pelmatochromines except *Pterochromis* (see p. 191).

Included species. Pelmatochromis buettikoferi Steindachner, 1894; *P. ocellifer* Boulenger, 1899; and *P. nigrofasciatus* (Pellegrin), 1900. For synonymies of these species see Trewavas (1973); in that work no mention is made of *P. corbali* (Blgr), 1913, which Thys (1968*a*) thought to be '. . . very nearly related and probably identical' with *P. buettikoferi*.

PTEROCHROMIS Trewavas, 1973

TYPE SPECIES. *Pelmatochromis congicus* Boulenger (1897)

SYNONYMY. *Pelmatochromis* (in part): Pellegrin, 1904; Boulenger, 1915; Regan, 1922; Thys, 1968*a*. In all, only the species *congicus* is involved.
Tilapia (in part): Thys, 1968*b* (the species *congicus* only).

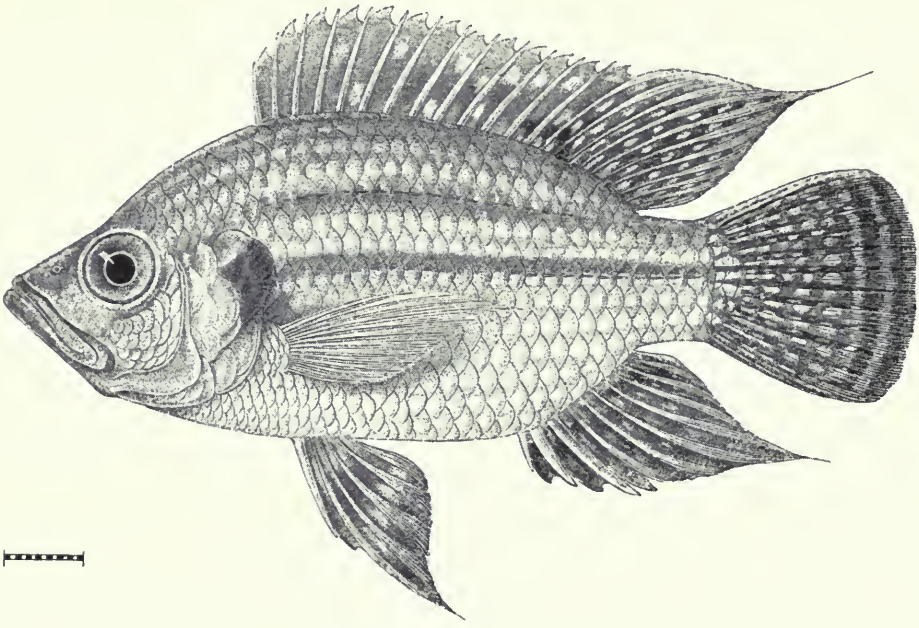

Fig. 7 *Pterochromis congicus*. From Boulenger, 1915; about natural size.

GENERIC STATUS AND RELATIONSHIPS. Thys (1968*a*) treated *congicus* as a species of *Pelmatochromis* but did not include it in any of his named subgeneric divisions. He did, however, group it with *P. ocellifer* (= *P. nigrofasciatus*, see Trewavas, 1973) and *P. ruweti* (now *Tilapia ruweti*), and indicated a possible relationship of the group with *Tilapia sparrmanii* (Thys, 1968*a*:381 and fig. 17). Later that year, Thys (1968*b*) formally included *P. ocellifer* and *P. congicus*, together with *P. buettikoferi* as a subgenus (*Pelmatochromis*) of *Tilapia; P. ruweti* was placed in the nominate subgenus *Tilapia*, together with *T. sparrmanii*.

Trewavas (1973) disputed Thys' reasoning (except that for including *P. ruweti* in *Tilapia*) and resurrected *Pelmatochromis* as a genus for the species *buettikoferi, ocellifer* and *nigrofasciatus* (see p. 143 above). Since, in her view, the species *congicus* could not be grouped with the other three species, and was not congeneric with any other taxon, she erected the genus *Pterochromis* for it alone.

I would concur both with Trewavas' view on the need to separate *congicus* from the other three

Pelmatochromis species, and with the generic status she accorded it. But, I would not support her contention that *Pterochromis congicus* '. . . is a specialised form' derived from *Pelmatochromis nigrofasciatus*, a relationship originally proposed by Thys (1968*a*; but see Trewavas [1973:10] regarding Thys' confusing *P. nigrofasciatus* with *P. ocellifer*, the latter name being used when he suggested the relationship of *P. congicus*).

Discounting the near impossibility of identifying an actual ancestral species, *Pterochromis congicus* and *Pelmatochromis nigrofasciatus* (or for that matter any *Pelmatochromis* species) have no shared derived features which might indicate their shared common ancestry. The resemblances rest almost entirely on symplesiomorphic characters, as for example the low vertebral counts, the *Tilapia*-type neurocranial apophysis, the presence of a *Tilapia*-spot in young fishes, a sessile prepharyngeal pad, microbranchiospines being present, the position of the upper lateral-line relative to the dorsal fin base, the size of the scales (27–28 in a lateral series), the elongate first pelvic fin ray, and the sexually monomorphic caudal fin shape.

Apart from its autapomorphic features (see below), *Pterochromis* has two characters, cycloid scales and unicuspid outer row jaw teeth, which could be considered apomorphic, and which are also shared with *Pelmatochromis* (and other taxa outside the pelmatochromine assemblage as well). The polarity and significance of these characters are discussed on pp. 143–145. If it be accepted that both are apomorphies, then their widespread occurrence amongst African cichlids reduces their value as indicators of recent shared common ancestry, especially when no other and congruent synapomorphies are shared by the taxa under review. In the case of *Pterochromis* and *Pelmatochromis* there are apparently no such congruencies. The presence of unicuspid teeth and cycloid scales in *Pterochromis* could as well indicate relationship with *Hemichromis* as with *Pelmatochromis* if comparisons are limited to west African taxa, and could even indicate affinity with taxa in other parts of the continent. But in every instance there are no features to support that relationship, and several characters to refute it.

Some of the characters used by Trewavas (1973) to distinguish *Pterochromis* from *Pelmatochromis*, namely the long, slender gill-rakers, the long ascending processes of the premaxillae and the elongate lower jaw, would at first glance seem to be apomorphic features.

Chief amongst these are the gill-rakers. Long, slender, untoothed, and numerous gill-rakers in the outer row of the first ceratobranchial are of uncommon occurrence in the Cichlidae, both African and Neotropical. They are not found in those African taxa which, on the basis of their few derived features, are taken to represent a plesiomorphic morphotype; for example *Heterotilapia multispinus* (see Oliver, 1984), *Pelmatochromis* (see p. 153) and *Astatotilapia* (see Greenwood, 1979 & 1980). However, long and slender rakers are common in other percoid groups, including members of the Labroidei, the suborder in which cichlids are currently classified. In most of these species, however, the rakers are tooth-bearing, as they are in the neotropical cichlid *Cichla* (whose derived or primitive status is disputed; see Stiassny, 1982).

Thus, the gill-rakers in *Pterchromis* could be interpreted as a plesiomorphic feature, but one showing partial derivation since the teeth are lost. Alternatively, the gill-rakers could be neomorphs which, in most respects, mimic the primitive condition. For the moment I see no means of resolving that ambiguity other than by applying the principle of parsimony, and concluding that the feature is indeed a plesiomorphic one.

Likewise I find difficulty in assessing the polarity of the probably correlated features of long ascending processes on the premaxillae, and a long lower jaw. Both are characters which occur in African cichlids and in out-group percoids as well. The upwardly inclined mouth (a feature not necessarily correlated with the elongate lower jaw and long premaxillary process) would, on the basis of both out- and intragroup comparisons, seem to be an apomorphy, albeit one which has evolved on several occasions.

One group of characters, the nature of the lower jaw dentition and dental arcade, not used by Trewavas (1973) in her generic diagnosis but noted in the generic description, is clearly an autopomorphy for *Pterochromis*. In that jaw the outer teeth situated anteriorly and immediately anterolaterally are several times larger and coarser than other teeth in the row, and are somewhat procumbently implanted. Their distinction is enhanced by the shape of the dental arcade which is noticeably angled mediad for a short section of its length immediately behind the enlarged anterior

teeth. Indeed, the small unicuspid teeth in that sector of the outer row seem to be continuous with the outermost row of inner teeth. This impression is enhanced both by the rather irregular serial arrangement of the inner teeth, and by those teeth being restricted to a transverse arc across the anterior and anterolateral part of the dentary.

Once again, as is so often the case with cichlid fishes, the characters which serve to distinguish a taxon give no indications of its phyletic relationships.

DIAGNOSIS. As for *Pelmatochromis* (p. 148) except that:

i. The unicuspid outer-row jaw teeth are relatively coarser in the upper jaw, and have only slightly recurved tips. In the dentary, the outer teeth situated anteriorly and immediately anterolaterally are much larger and coarser than the succeeding teeth in the row, and are implanted so as to slope forwards; the anterior teeth are somewhat isolated from the others since anterolaterally the row has a noticeable, and rather abrupt, mediad inclination, thus appearing to become continuous with the outermost row of the inner tooth-series (see fig. 8 in Trewavas, 1973).

ii. The mouth (Fig. 7) is inclined upwards at a noticeable angle (*ca.* 45° to the horizontal). The ascending processes of the premaxillae are long (42–44 percent of head length), their tips reaching a point just before the anterior tip of the supraoccipital and lie above about the centre of the orbit; lower jaw also long (50–55 percent of head length).

iii. Upper lateral-line, at its highest point, separated from the dorsal fin base by $3\frac{1}{2}$ or 4 scales; posteriorly there is one large and one very small scale between the last two pored scales and the dorsal fin base.

iv. Gill-rakers in the outer row of the first ceratobranchial are numerous (17–19), long, smooth and fine (i.e. flattened, bristle-like structures), and are implanted at approximately right angles to the surface of the arch. Rakers on the first epibranchial are slender, but are shorter proximally; arranged in two rows, with 9–11 in the outer row.

v. 13 abdominal and 12 caudal vertebrae (total count 25).

vi. Dorsal fin with 13–14 spines.

vii. *Tilapia*-spot on the dorsal fin but no indications of a *Pelmatochromis*-spot (see p. 143).

viii. Breeding habits unknown.

NOTES ON THE ANATOMY AND OTHER FEATURES. Because so little study material is available, few observations could be made on the soft anatomy or the osteology of *Pterochromis congicus* (the sole representative), other than those which can be gleaned from superficial dissections and from radiographs.

Judging from the latter, the *neurocranium* has an outline very similar to that of *Pelmatochromis buettikoferi* (see p. 149, and Fig. 3). The ethmovomerine region is short and moderately decurved, and the supraoccipital crest is high, with its anterior part extending to a point over about the middle of the orbit. The apophysis for the upper pharyngeal bones, examined by dissection, is of the *Tilapia*-type (Greenwood, 1978).

The *infraorbital bone series* is complete, the lachrymal a long and relatively shallow bone with four openings to its laterosensory canal; the second infraorbital barely overlaps the posterior flange of the lachrymal.

No details of the *palatoquadrate arch* and the *suspensorium* could be seen from the radiographs, but a limited dissection showed a double palato-ethmoid articulation of the common cichlid kind (see Greenwood, 1985*a*:133–134 and 137–140). There are seven laterosensory canal openings on the *preoperculum*.

The *jaws*, apart from the long premaxillary ascending processes, and the peculiar dental arrangement in the dentary (see p. 155), provide no obvious points of comment which could be detected from a radiograph or which are visible externally. The passage of the laterosensory canal through the anguloarticular is roofed.

There are 13 abdominal and 12 caudal *vertebrae* (excluding the fused PU1 and U1 centra) in the two specimens radiographed; in one of these a large, well-developed spondylophysial apophysis is visible on the third centrum. As seen radiographically, the *caudal skeleton* has no distinctive features.

Little is known about the *branchial skeleton*, including the *pharyngeal jaws*. The lower pharyngeal bone is figured by Trewavas (1973: fig. 7). The upper elements have the same shape and spatial relationships as were described for *Pelmatochromis* (p. 151), and must be considered of the generalised and plesiomorphic cichlid type.

Squamation. Body scales in *Pelmatochromis congicus* are large and obvious; those on the chest have a gentle size-gradient with the scales on the ventrolateral aspects of the flanks, and although smaller are not noticeably so. Anteriorly, the upper lateral-line at its highest point (over the 8th pored scale) is separated from the dorsal fin base by $3\frac{1}{2}$ or 4 scales; posteriorly, the last two pored scales are separated from the fin base by one large and one very small scale. Save for a small naked area anteroventrally, the cheek is covered by three rows of scales.

Fins. There is apparently no sexual dimorphism in the shape of the caudal fin margin, which is very gently rounded. The first pelvic fin ray is clearly the longest.

With so few specimens known, it is impossible to be certain about the absence of sexual dimorphism in caudal and pelvic fin shapes, or of the significance to be attached, in that context, to the filament-like elongation of certain posterior rays in the dorsal and anal fins.

Relationships. There are no features which indicate that *Pterochromis* is closely related to any other pelmatochromine taxa, or on current evidence, to any other African lineage. Phylogenetically speaking it must be considered *incertae sedis*.

Included species: the type and only species *Pterochromis congicus* (Blgr) 1897.

II Pelmatochromines without microbranchiospines, and with a visor-like hanging pharyngeal pad

All taxa included in this pelmatochromine subdivision have a typical, visor-like and well-circumscribed projection of the pharyngeal tissues situated immediately anterior to the upper pharyngeal bones of each side (see p. 142; also Trewavas, 1974; Greenwood, 1983).

As conceived here, this subgroup also contains an assemblage which Thys (1968*a*:365, his species 17–21) maintained have '. . . a feebly developed or even no hanging pad on the roof of the pharynx'. I cannot agree with Thys on this point; specimens of all the named species he mentions (and one unnamed species, no. 21) have a distinctly visor-like pad. The pad is seemingly subject to the vagaries of preservation and curation (and possibly by the condition of the live fish too), and it can show intraspecific variability in its prominence. But, in its basic form and clear circumscription

Fig. 8 Dentary teeth (right) of *Pelvicachromis pulcher* to show characteristic shape of chromidotilapiine teeth; seen in near lateral aspect. Magnification × 29 (BMNH 1901.11.28:13–20; a syntype).

Fig. 9 Right dentary of *Pelvicachromis humilis* to show the characteristic chromidotilapiine feature of the posteriorly directed teeth situated anterolaterally on that bone (BMNH 1972.3.16:8–10). Magnification × 14.

from the surrounding pharyngeal tissue, it is always apparent in the specimens and species I have examined.

Microbranchiospines are absent in all members of group II pelmatochromines, a condition which is not necessarily correlated with the presence of a hanging pad since both structures are present in other cichlid genera (see Greenwood, 1983:267).

Both the presence of a hanging pad, and the absence of microbranchiospines can be ranked as synapomorphic features for this pelmatochromine group (see p. 191). Two other characters can be treated as congruent synapomorphies.

Throughout the size-range of specimens available to me, the outer row jaw teeth are characteristically shaped unicuspids. Unfortunately, those size ranges cover few small specimens of any species, and thus it has proved possible to trace the ontogenetic history of tooth form in only one species. No published information on that point is available either. In the exceptional species, *Chromidotilapia kingsleyae* (see p. 168), specimens 30–35 mm SL do have some teeth in which a very weak shoulder (see p. 145) is present, suggesting that at least weakly bicuspid teeth may precede the definitive and characteristic unicuspids of larger individuals.

The characteristic group feature of the definitive outer row jaw teeth concerns the shape of the crown. Whereas in *Pelmatochromis* and *Pterochromis* the crown is an attenuated cone (see Fig. 1), in this group it can be described as a unilaterally compressed cone, the compression being manifest on the labial aspect of the crown (Fig. 8). That is to say, in cross-section its labial face, relative to the lingual one, is flattened, although its surface is still clearly curved. As a consequence of this differential flattening, the anterior and posterior margins of the crown, especially near its tip, are relatively acute and ridge-like, not rounded as they would be in a uniformly conical one, and the crown comes to resemble the tip of a surgical suture needle. As compared with the crown of the teeth in *Pelmatochromis*, and especially that in *Pterochromis*, this part of the tooth in all group II pelmatochromines is more strongly recurved.

The second derived feature concerns the orientation, on both sides of the dentary, of the first few (1–4) teeth occupying an anterolateral position in the outer tooth row of that bone. In these teeth the curvature of the crown is directed posteriorly and not buccally as it is in all other teeth of the row (figs 9 & 10). Occasionally, in one species, the atypically orientated teeth occur unilaterally,

and there are indications in *Thysia* that such teeth appear late in the ontogenetic succession of tooth forms since posteriorly directed teeth are found only in specimens more than 95 mm SL.

A third derived feature, the form of the gill-rakers on the first ceratobranchial, is present in group II fishes, but its status as an autapomorphy is questionable; it could be a synapomorphy shared

Fig. 10 Right dentary (in part) of *Pelvicachromis pulcher* to show posteriorly directed anterolateral teeth and the general morphology of chromidotilapiine teeth (same specimen as Fig. 8). Magnification × 14.

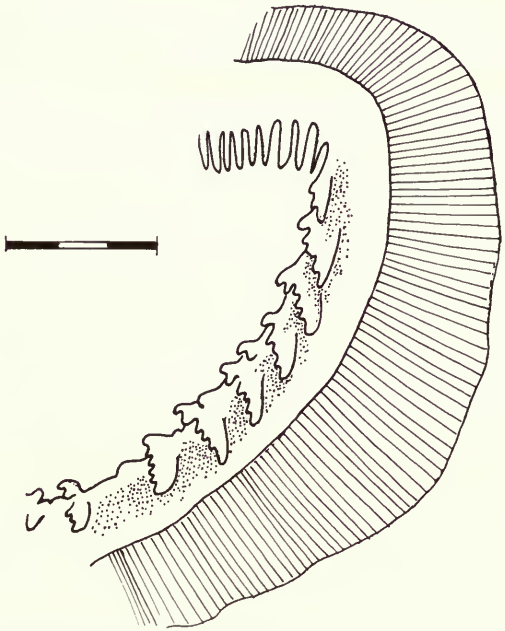

Fig. 11 Partially schematic drawing to show the general morphology of the gill-rakers on the first arch of a chromidotilapiine species. Modified after Trewavas (1974).

with *Pelmatochromis* (see p. 145). Basically, gill-raker morphology in both groups is similar (Fig. 11), the rakers being markedly pachydermatous, crescentic in shape, aligned transversely across and close to the arch, their tips produced into a horn-like projection, and the concave upper surface of the raker thrown into a number of low projections. Also common to both groups are the projections developed from the median membrane, and which are positioned between the rakers of the inner and outer rows. Again as in *Pelmatochromis*, the shape of the epibranchial rakers, as compared with the lower elements, is distinctly different, being dagger- or spear-shaped and inserted almost perpendicularly to the arch. However, in group II pelmatochromines the epibranchial rakers are reduced to a single row over much of that bone. Presumably the presence of a hanging pad contiguous with the proximal part of the arch inhibits the development of rakers in that region because a short inner row is present distally on the epibranchial.

In general, the outer row ceratobranchial rakers of group II species are thicker (i.e. more pachydermatous) than in *Pelmatochromis*, the upper surface is usually more tuberculate, and the distal tip appears more protracted and horn-like.

One other but polythetic feature may be an autapomorphy for group II pelmatochromines, and is discussed on p. 191.

On the basis of all constituent taxa sharing the apomorphic features discussed above (but with great reservation about the autapomorphic status of the gill-rakers), I would treat the group II species as a monophyletic assemblage. The possible relationships of that assemblage to *Pelmatochromis,* and the interrelationships of its constituent genera are discussed later (p. 191).

With one exception (the species *ansorgii,* see below) all the taxa treated here as members of group II, were placed by Thys (1968*a*) in one or other of three named subgenera, *viz. Chromidotilapia, Pelvicachromis* or *Nanochromis,* taxa raised to generic level by Thys' and other's subsequent revisions (see Thys, 1968*b*; Trewavas, 1973, and p. 140 above). Certain species described after 1968 have been placed by their authors (Thys & Loiselle, 1971; Trewavas, 1973 & 1974; Roberts & Stewart, 1976; Stewart & Roberts, 1984) in one or other of these genera. *Pelmatochromis ansorgii* Blgr, the taxon of uncertain subgeneric affinity in Thys' (1968*a*) revision was chosen as the type species for a new genus described by Loiselle & Welcomme in 1972, and will be considered first.

THYSIA Loiselle & Welcomme, 1972

TYPE SPECIES. *Pelmatochromis ansorgii* Boulenger, 1901

SYNONYMY. *Pelmatochromis* (in part): Pellegrin, 1904 (*ansorgii* only); Boulenger, 1915 (*ansorgii, annectens* and *arnoldi*); Regan, 1922 (*ansorgii, annectens* and *arnoldi*); Thys, 1968*a* (*ansorgii* with which *arnoldi, annectens* and *maculifer* were synonymised).
Tilapia (in part): Ahl, 1939 (the species *maculifer*, see Thys, 1968*a*).

A description of the two *Thysia* species, *Thysia ansorgii* (Blgr) and *Th. annectens* (Blgr), together with extensive notes on their biology, is given by Loiselle & Welcomme (1972), although few anatomical details are discussed.

DIAGNOSIS. *Thysia* is distinguished from other African taxa by the following characters taken in combination. Body moderately deep, not fusiform (Fig. 12).

Neurocranial apophysis for the upper pharyngeal bones formed from the parasphenoid only (i.e. of the *Tilapia*-type; Fig. 13B) supraoccipital crest prominent; supraethmoid and vomer in contact.

Palatine with a two-point neurocranial contact, anteriorly through an articulation in the region of the ethmovomerine suture, and posteriorly with the ventral face of the lateral ethmoid (see Greenwood, 1985*a*); a calyx present between the metapterygoid and the hyomandibula.

A well-developed and circumscribed, visor-like hanging pad developed from the buccopharyngeal roof immediately anterior to the upper pharyngeal bones. Posterior facing margins of the major upper pharyngeal bones (the fused 3rd and 4th pharyngobranchials) forming a broad, shallow V, its apex directed anteriorly (Fig. 4A). No 'kukri'-shaped teeth on the lower pharyngeal bone (see p. 197 and Fig. 30), the teeth of which all have the tip of the major cusp pointing forwards

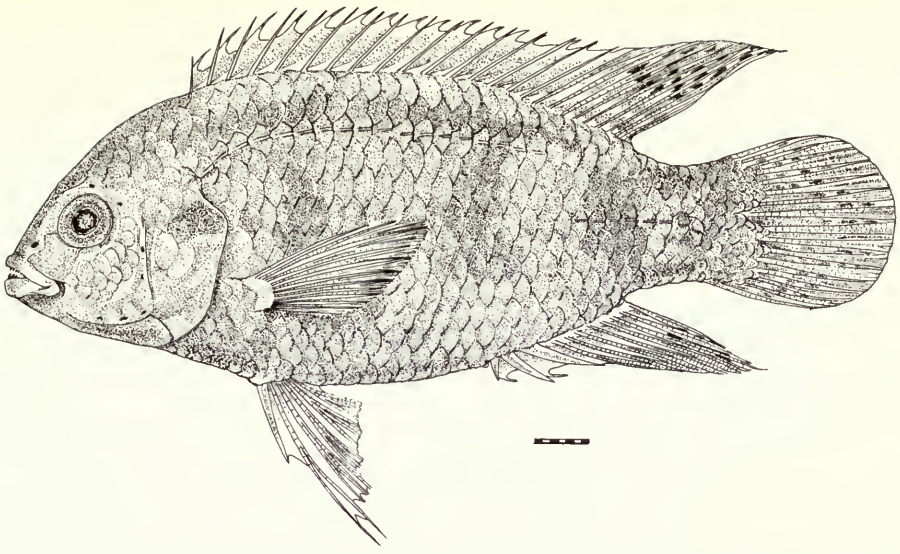

Fig. 12 *Thysia ansorgii*. One of the syntypes (BMNH 1901.1.28:9–12); scale bar in mms. Drawn by Gordon Howes.

and lying a little anterior to, or in the same vertical as the tooth's posterior margin. Anterior blade of the lower pharyngeal bone short, its length contained about 4 times in the overall length of the bone.

Infraorbital bones forming a complete lower and posterior margin to the orbit, the first infraorbital (lachrymal) with 4 openings to its laterosensory canal.

Outer row jaw teeth, at least in specimens over 40 mm SL, unicuspid and with crowns of the compressed-conical type (see p. 158; Fig. 8); in fishes over 95 mm SL, a few (1–4) teeth situated anterolaterally in the lower jaw are aligned so that the crown points posteriorly, not bucally like the other teeth (see p. 158; Fig. 8).

Lower jaw less than 50 percent of head length. Anguloarticular with a roofed canal for the passage of the mandibulo-preopercular laterosensory canal.

Scales cycloid, 25–30 in the lateral-line series. Upper lateral-line clearly separated from the dorsal fin base over its entire length, and by $2\frac{1}{2}$–3 scales at its highest point (i.e. the 8th or 9th pored scale in the series), and by one small and one large scale over the last 2–4 pored scales. Cheek almost entirely covered by 3 or 4 rows of scales, but with a small naked area anteroventrally. Chest scales not noticeably smaller than those situated anteroventrally on the flanks and belly; 16 scales around the caudal peduncle.

Gill-rakers on the ceratobranchial of the first arch pachydermatous, elongate and crescentic, orientated almost transversely across the arch, and closely applied to its surface; upper surface of the rakers tuberculate; distal tip produced and horn-like (see p. 160); 8–11 in number. A single row of dagger-like rakers on the upper part of the epibranchial. Microbranchiospines absent on all arches.

Total vertebral counts 25 or 26, comprising 13 abdominal and 12 or 13 caudal elements (the fused PU1 and U1 centra excluded from all counts). A single, well-developed supraneural (predorsal) bone is present.

Dorsal fin with 13–16 spines, anal with 3. Sexual dimorphism in the shape of the caudal fin margin, whose upper half projects further posteriorly in adult males than in females. Pelvic fin with the first ray longest in both sexes, and greatly produced in sexually active males. No *Tilapia*-spot; substrate guarder (Loiselle & Welcomme, 1972).

NOTES ON THE ANATOMY AND OTHER FEATURES. Anatomical and osteological studies were made on the type species, *Th. ansorgii* only, but comments on dental features include *Th. annectens* as well.

Like *Pelmatochromis*, most anatomical features in *Thysia* depart in no significant way from the modal condition in other African species.

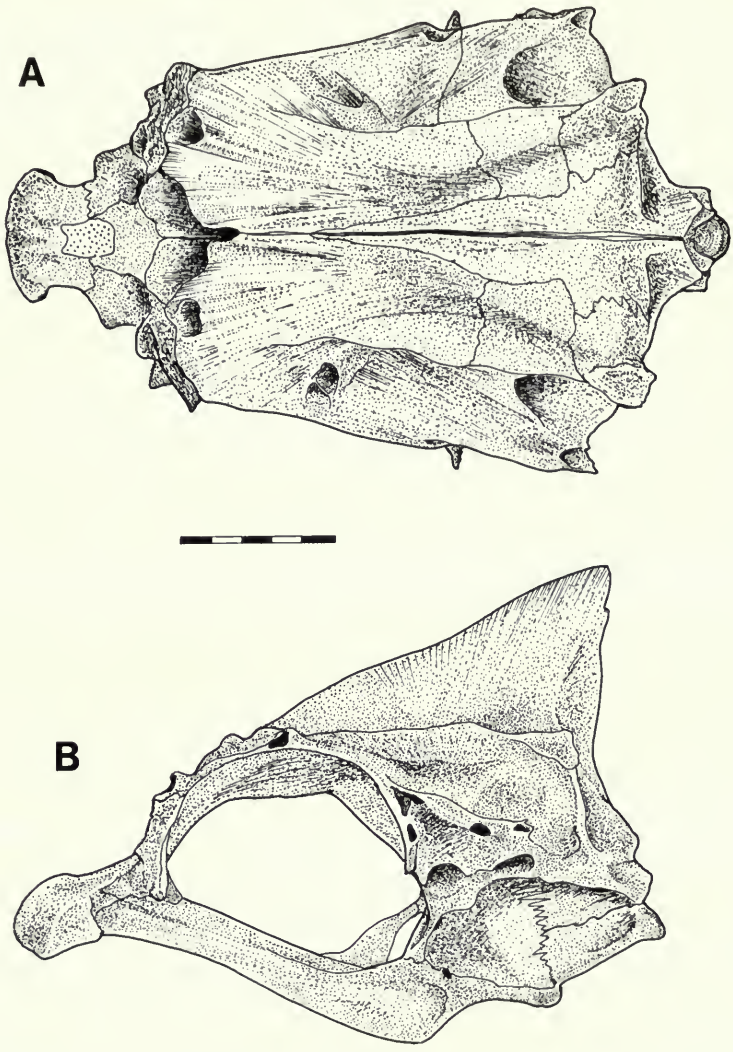

Fig. 13 Neurocranium of *Thysia ansorgii* in A. Dorsal; B. left lateral view. Scale bar in mms (BMNH 1977.11.8:430–455).

The *neurocranium* (Fig. 13) is generally similar to that in *Pelmatochromis buettikoferi* (p. 149). The supraoccipital crest is tall, the neurocranial apophysis for the upper pharyngeal bones is of the *Tilapia*-type, as is the lateral commissure (see Greenwood, 1986) but in *Thysia* there is no precommissural bridge although well-developed precommissural spurs are present on the prootic. The skull of *Thysia* differs, however, in having a slightly broader interorbital region (width contained about twice in the neurocranial length, as compared with $2\frac{1}{3}$ times in *P. buettikoferi*), and the anterior tip of the supraoccipital extends further forward to a point above the anterior third of the

orbit; also, the ethmovomerine skull region is a little shorter in *Thysia* than in *Pelmatochromis* ($3\frac{3}{4}$times in neurocranial length cf. $3\frac{1}{4}$ times) and slopes less steeply (*ca.* 30° to the horizontal, cf. 50° in *P. buettikoferi*), and the supraethmoid is suturely united with the vomer.

The *infraorbital series* is complete, and the lachrymal has four openings to its laterosensory canal system. Somewhat more than the anterior third of the 2nd infraorbital overlaps the posterior shelf of the lachrymal (see Fig. 5E).

In the *pharyngobranchial skeleton*, the fourth epibranchial has a well-developed shank ridge which is almost spinous, and its quadrangular area is elongate and near-rectangular (see Greenwood, 1985*a*). There is a prominent and expansive cartilaginous extension from the anterior margin of the 2nd epibranchial; in one of the two specimens dissected the projection is almost square, in the other it is anvil-shaped.

The *upper pharyngeal bones*, and their arrangement, are similar to those in *Pelmatochromis*, and the lower bone closely resembles that of *P. buettikoferi* in its shape, proportions and dentition. In most respects the drawing of the lower pharyngeal bone in Loiselle & Welcomme (1972: fig. 4, which cf. Fig. 6B) is inaccurate, particularly with regard to the depiction of a deep median depression in the posterior margin, short and triangular articulating horns, and the somewhat 'waisted' appearance of the dentigerous surface.

The *vertebral column* is made up of 13 abdominal and 12 or 13 caudal vertebrae (the fused PU1 and U1 centra excluded); there is a single and slender supraneural bone.

No outstanding features were noted in the skeleton of the *caudal fin*. Likewise the *suspensorium, palatoquadrate arch* and the *jaw skeleton* show no obvious departure from the usual African cichlid condition. There is a well-developed calyx, open medially, formed from the metapterygoid and hyomandibular bones, and the palatine has a two-point articulation with the ethmovomerine region of the skull (see Greenwood, 1985*a*). In the preoperculum and the dentary there are, respectively, 7 and 5 openings to the laterosensory canals; the anguloarticular has a roofed passage for the mandibulo-preopercular canal.

Myology and arthrology of the jaws and palatoquadrate arch. Once again, there are no basic differences between *Thysia* and *Pelmatochromis*, although the relative sizes of certain muscles differ a little in the two taxa, and there is a smaller area of fusion between the A1β and Aw tendons in *Thysia* (see p. 158). All in all, however, the conditions are those of the generalised African cichlid type.

Dorsal and ventral gill-arch musculature is essentially like that of *Pelmatochromis*, but in *Thysia* no part of the *levator posterior* muscle inserts on the articular horn of the lower pharyngeal bone, and the insertion of the *levator externus* 4 muscle is merely a thin, tendinous thread. In the two latter characters *Thysia* shows the plesiomorphic condition for these muscles amongst cichlids, but it is not alone in so doing.

As in *Pelmatochromis* (and many other African cichlids; see Anker, 1978; Greenwood, 1985*a*) the *rectus ventralis* muscle inserts entirely on the semicircular ligament, whilst *obliquus ventralis* 3 has the greater part inserted on the third hypobranchial, only a thin posterolateral section joining the ligament. The *transversus ventralis anterior* muscle is interrupted medially by the anterior blade of the lower pharyngeal bone.

Squamation. Between the highest point in the upper lateral-line (i.e. about the 8th and 9th pored scale) and the dorsal fin base there $2\frac{1}{2}$ or 3 scales, and between the last 2–4 pored scales and the fin there is one large and one very small scale. The chest is fully scaled, with the scales in that region not noticeably smaller than those on the venter. A small naked area occurs anteroventrally on the cheek which is otherwise fully scaled. As in the majority of African cichlids there are 16 scales around the caudal peduncle.

Fins. The lower rays in the upper half of the caudal fin are produced in adult males, with the result that the fin's posterior margin is irregular; in females, although the margin is regular, it is slightly extended around its midpoint.

In both sexes the first pelvic ray is the longest (albeit only slightly longer than the second ray in a few of the juveniles and adults examined). Adult males have the first ray greatly produced and filament-like (see fig. 1 in Loiselle & Welcomme, 1972).

Coloration. Loiselle & Welcomme (1972) give a detailed colour description, and there are good

colour photographs in Voss (1977; 1980) and Linke & Staeck (1981). A noteworthy feature in sexually active females is the presence of a prominent silver spot on the venter immediately above the ano-genital region.

Biology. Various aspects of *Thysia* biology, including its breeding behaviour and colour changes, are described by Loiselle & Welcomme (1972) and Voss (1977; 1980).

Relationships. The relationship of *Thysia* amongst the pelmatochromine fishes will be discussed in detail later (p. 191).

Its possible close relationship with *Hemichromis* and '*Pelmatochromis' thomasi* (now *Anomalochromis thomasi*; see Greenwood, 1985*b*) was suggested by Loiselle & Welcomme (1972); that idea is discussed, and discounted, in Greenwood (1985*a* & *b*).

In their paper Loiselle & Welcomme also argued that *Thysia* was not '. . . closely related to either the *Nanochromis-Pelvicachromis* complex or to *Chromidotilapia*', a conclusion very much at odds with that arrived at here (see p. 191). Several of the features in *Thysia* which Loiselle & Welcomme used in their argument (head shape, degree of jaw prostrusibility, position of the mouth, coloration) are not applicable to the question of overall relationship, but are concerned more with autapomorphic specialisations and thus with a low (e.g. generic or specific) level of classification. They do, however, comment on two characters (gill-raker morphology, and the pharyngeal pad) which I would consider to be of importance in establishing wider levels of interrelationship. Regarding gill-rakers, Loiselle & Welcomme (1972:54) indicate that those of *Chromidotilapia* differ from the rakers in *Thysia*, a conclusion with which I would not agree, especially since the feature they stress (tuberculation) is one most susceptible to the effects of preservation (p. 146). In my view, the overall gill-raker morphology, and indeed its more detailed aspects, are very similar in the two taxa, and can be considered as a unifying synapomorphy at the suprageneric level for these and other taxa (p. 191). Likewise, I do not agree with Loiselle & Welcomme's idea that, as compared with *Thysia* the hanging pad in *Nanochromis* is '. . . rudimentary' (*op.cit.*:55). Again, there is the possibility of preservation artefacts, but in none of the *Nanochromis* material I have examined would I describe the pad as rudimentary or in any way less well-developed than it is in *Thysia*.

CHROMIDOTILAPIA Boulenger, 1898

TYPE SPECIES: *Chromidotilapia kingsleyae* Boulenger, 1898 (by original designation).

SYNONYMY. *Pelmatochromis* (part): Pellegrin, 1904 (the species *kingsleyae, guntheri* and *pellegrini* [a junior synonym of *guntheri*; see Boulenger, 1915]); Boulenger, 1915 (*kingsleyae, guntheri*, and *nigrofasciatus* in part [the species *batesii*, treated as a synonym]); Regan, 1922 (the species included by Boulenger, 1915 above).

Pelmatochromis (*Chromidotilapia*) in part: Thys, 1968*a* (the species *guntheri, kingsleyae, batesii* and *schoutedeni*).

Chromidotilapia (part): Boulenger, 1898 (the species *kingsleyae* only); Trewavas, 1974 (*kingsleyae, guntheri* [with which *loennbergi* was included as a subspecies], and *finleyi*).

The genus *Chromidotilapia* was first described by Boulenger (1898) for his new species *kingsleyae*, (Fig. 14) although he did include, tentatively, another species, *C. frederici* (Castelnau). The latter, under a *nomen novum*, is now considered to be a *Serranochromis* (see Bell-Cross, 1975; Greenwood, 1979:304).

Interestingly, among the diagnostic features for *Chromidotilapia*, Boulenger (1898) noted that some of the lower jaw teeth had their unicuspid crowns directed posteriorly and not buccally, a feature now known to characterise all member taxa of the group II pelmatochromines (see p. 158).

Some six years after Boulenger erected this genus, Pellegrin (1904) synonymised it with *Pelmatochromis*, but gave no reasons for so doing. Regan (1922) followed Pellegrin, but again without comment or explanation. Thys (1968*a*), however, resurrected the taxon as, at least temporarily, a subgenus of *Pelmatochromis*.

With Thys' (1968*b*) inclusion of the nominate subgenus of *Pelmatochromis* in *Tilapia*, the subgenus *Chromidotilapia* regained its former generic status, at least by implication, and was formally confirmed therein by Trewavas (1974:388–389).

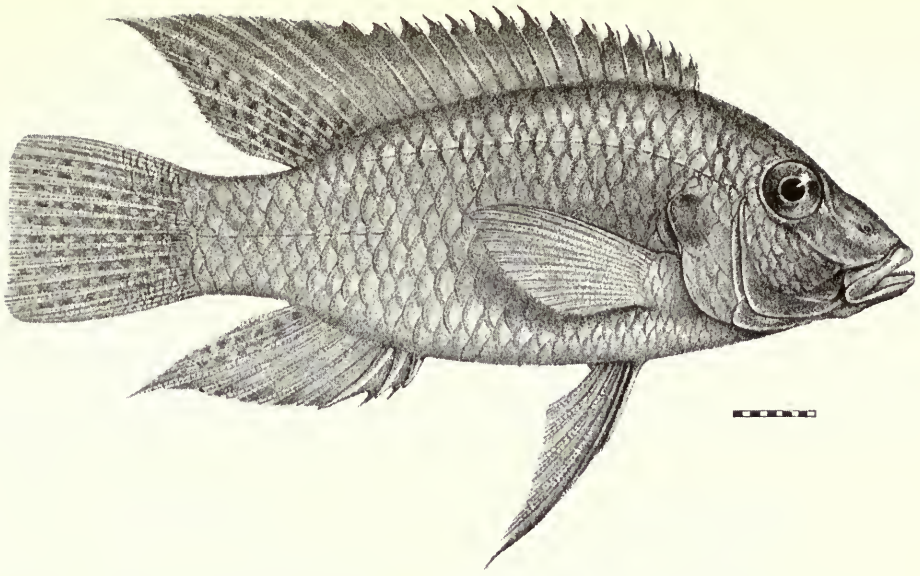

Fig. 14 *Chromidotilapia kingsleyae*. Holotype; from Boulenger, 1898. Scale bar in mms.

Thys' diagnosis for *Chromidotilapia* is based on (1) The well-developed hanging pad in the pharynx; (2) The broad and tuberculate gill-rakers in the outer row of the first gill-arch (which rakers he considered to have all tubercles of about the same size); (3) No sexual dimorphism in the shape of the caudal fin, which has a subtruncate posterior margin in both sexes; (4) The absence of microbranchiospines; (5) The first pelvic fin ray is the longest in both sexes.

Trewavas (1974) provided some data on intraspecific variability in gill-raker morphology, but did not comment on its relevance to Thys' diagnostic features for the genus, which she accepted without comment.

I have reservations about the significance and value of the gill-raker tuberculation character used by Thys since there is considerable interspecific and some intraspecific variability in this feature amongst the *Chromidotilapia* species I have examined. There is also the problem associated with *post-mortem* changes and with preservation induced variation (see p. 146).

Questions relating to autapomorphies and hence generic status amongst the pelmatochromines, especially those involving group II taxa, will be discussed later. For the moment it will suffice to note that none of those used by Thys can be considered autapomorphic for the genus.

Parenthetically it should be noted here that Trewavas (1974:395) mentions a species, *C. caudifasciatus*, which she considers is close to *Chromidotilapia batesii*. Nowhere else in her paper does she mention *C. caudifasciatus*, and I can only assume that the reference is to the species *caudifasciatus* of Boulenger (1913), which Thys (1968*a*:367 and 380) included in his subgenus *Nanochromis* of *Pelmatochromis*. That species is considered later in this paper (p. 174), and certainly does not appear to be a *Chromidotilapia*.

DIAGNOSIS. As for *Thysia* (p. 160) except for: (1) Lachrymal with 5 openings to its laterosensory canal in all but one species (where there are 4). (2) Although posteriorly directed outer teeth occur anterolaterally in the lower jaw, their presence is apparently restricted to large individuals; it is not known at what size they first appear. Similarly, it is not known at what size the typical compressed-conical teeth are first present (see p. 158). (3) Lateral-line series with 25–29 scales; at its highest point (about the 8th scale) the upper lateral-line is separated from the dorsal fin base by two large and one very small scale, or by only two large scales. The last five or six pored scales are separated from the

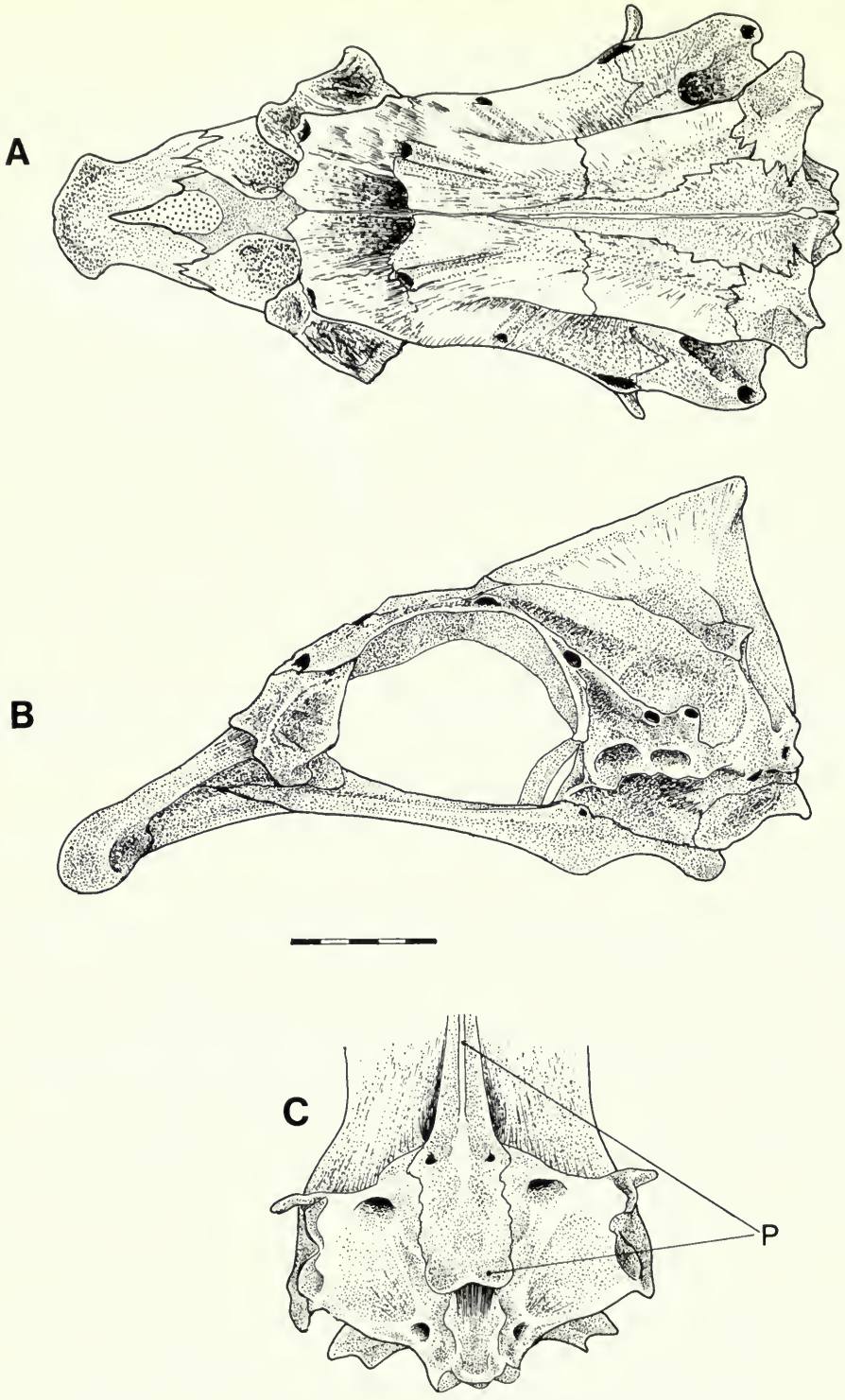

Fig. 15 Neurocranium of *Chromidotilapia kingsleyae* in: A. Dorsal; B. left lateral view. C. Neurocranial apophysis for the upper pharyngeal bones. P = parasphenoid. Scale bar in mms. (BMNH 1867.5.3:2).

fin base by one large and one very small scale. In some species the chest scales are slightly, but distinctly, smaller than those on the anteroventral aspects of the belly and flanks, but the size gradient between scales in the two regions is gradual; chest scales in other species as in *Thysia*. Cheek with 3 or 4 scale rows; in some species a narrow naked area anteroventrally. (4) Gill-rakers on the outer row of the first ceratobranchial are, in most species, more obtusely tuberculate than those in *Thysia*. (5) Caudal fin without any sexual dimorphism in the shape of its posterior margin, which varies from subtruncate to gently rounded. Dorsal fin with 14–17 spines, anal with 3. (6) Total vertebral count 24 or 25, comprising 12 (rare) —14 abdominal and 12 or 13 caudal centra (fused PU1 and U1 centra excluded). (7) Mouth brooder, at least during the later stages of brood care (see Myrberg, 1965; Thys, 1968*a*; Peters & Berns, 1978; Linke & Staeke, 1981). (8) Adult females with an extensive metallic (silvery to coppery) flush on the dorsal fin; no silvery blotch above the vent in females.

NOTES ON THE ANATOMY AND OTHER FEATURES. Dissections and osteological studies were made on *C. kingsleyae*, *C. guntheri* and *C. finleyi*.

There is some intrageneric variation in the overall morphology of the *neurocranium* Figs 15–17).

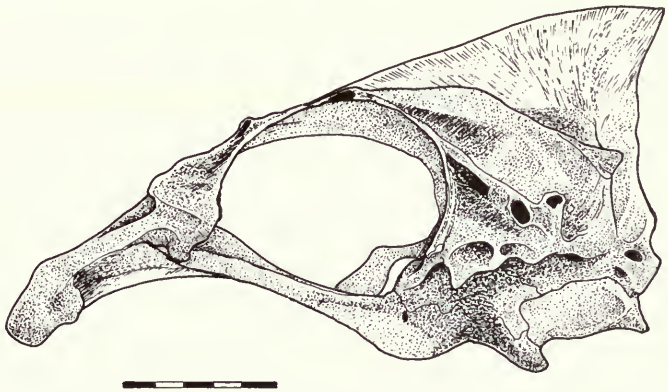

Fig. 16 Neurocranium of *Chromidotilapia guntheri loenbergi* in left lateral view. Scale bar in mms. (BMNH 1973.5.14:615–621).

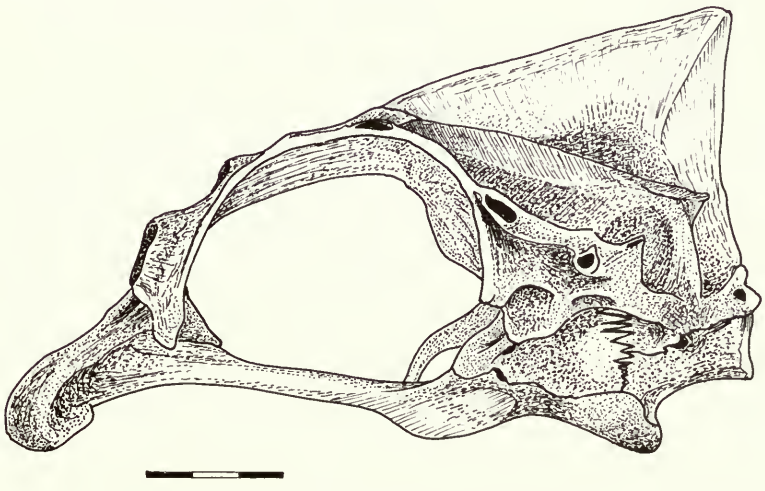

Fig. 17 Neurocranium of *Chromidotilapia finleyi* in left lateral view. Scale bar in mms. (BMNH 1973.5.14:544; one of the paratypes).

Chromidotilapia kingsleyae and *C. guntheri* have a more elongate and narrower skull than does *C. finleyi*; however, even in the comparatively foreshortened neurocranium of *C. finleyi*, the ethmovomerine region is relatively longer than in *Pelmatochromis* species (*ca* $3\frac{1}{2}$ times in neurocranial length cf. $3\frac{3}{4}$ times), and it is also somewhat narrower. This ethmovomerine attenuation is most extreme in *C. kingsleyae* and *C. guntheri*, where the region's length is contained about $2\frac{1}{2}$ to 3 times in neurocranial length. In both these species the ventral profile of the ethmovomerine skull region is noticeably elongate and decurved when compared with *Pelmatochromis*; even in *C. finleyi* the curvature and elongation is apparent. Skull width in *C. kingsleyae* and *C. guntheri* is less than in *C. finleyi* and *Pelmatochromis*. In all three *Chromidotilapia* species the supraethmoid and vomer are suturally united.

The *lateral commissure* can be of either the *Haplochromis*-type (*C. guntheri* and *C. finleyi*) or of an intermediate *Tilapia-Haplochromis* type in *C. kingsleyae*. A precommissural bridge is not developed in any species, but there are prominent precommissural spurs present ventrally on the prootic, and less obvious ones dorsally on that bone (Greenwood, 1986).

The *infraorbital series* (Fig. 5B) is complete. About two-thirds of the second infraorbital bone overlaps the posteriorly directed shelf of the lachrymal. The latter bone has a characteristic apron-like shape in all three species; its overall proportions are clearly rectangular in *C. kingsleyae* and *C. guntheri*, but are more nearly square in *C. finleyi*. The latter species also differs in having only four and not five openings to its laterosensory canal. Four openings are the commonest condition amongst pelmatochromines, and are thought to represent the plesiomorphic state in cichlids (see Trewavas, 1983; Oliver, 1984; Greenwood, 1985*a*).

In the *vertebral column* there are 12 (rarely) to 14 abdominal vertebrae (mode 13), and 12 (mode) or 13 caudal elements (excluding the fused PU1 and U1 centra), giving a total count of 24 (rare) to 26. In the two skeletons of *C. kingsleyae* available, and in the single skeleton of *C. batesii*, there is a strong and deep spondylophysial apophysis on the third abdominal centrum.

The *myology, arthrology and osteology of the jaws and pharyngobranchial region* in *Chromidotilapia* are, with few minor exceptions, like those in *Thysia* (see p. 163). The dorsal gill-arch musculature, examined in *C. guntheri* and *C. finleyi*, however, is more like that of *Pelmatochromis* than *Thysia* since there is a small musculose, rather than tendinous, slip of the fourth *levator externus* muscle inserting onto the fourth epibranchial, and a musculose attachment of the *levator posterior* muscle to the horn of the lower pharyngeal bone. In those respects, *Chromidotilapia* is more derived than is *Thysia*.

Due to inadequate material, little could be learnt about the extent to which the anterior cartilaginous flange on the *second epibranchial* is developed. In *C. finleyi* the flange is large and rectangular in outline. Judging from the available skeletal material the *pharyngobranchial skeleton* in *Chromidotilapia* shows no outstanding features (see also Greenwood, 1985*a*).

In the lower jaw, the tendon A1β of the *adductor mandibulae* I muscle is completely free from that of the Aw tendon, the usual condition in cichlids.

The ascending process of the premaxilla is, relative to the alveolar arm of the bone, longer in *Chromidotilapia* than in *Thysia*, and markedly longer than in *Pelmatochromis*.

The *dentition* in adult specimens of all species examined has both the compressed-conical unicuspid teeth typical of group II pelmatochromines, and the equally typical posteriorly directed anterolateral teeth in the dentary (see p. 158). Smaller fishes, however, have outer row teeth of a slightly different kind. In these, the crown has a less obviously flattened labial surface and consequently has less distinct sharp-edged margins to the crown. Smaller specimens also lack the posteriorly directed anterolateral dentary teeth. Furthermore, some 'shadow-shouldered' teeth or even distinctly 'shouldered' teeth (see p. 145) are present in both jaws, at least in specimens of *C. kingsleyae* less than 60 mm SL, and in *C. finleyi* of less than 50 mm SL. In both these species the figures given refer to the largest of the 'small' specimens available for study in which such teeth were observed, and thus may not truly reflect the minimum sizes above which a fully 'adult' dentition is present. Posteriorly directed anterolateral teeth are absent in the dentary of most *C. kingsleyae* specimens less than 50 mm SL, but are present in one fish of only 40 mm SL. The size range of the samples from which these data were derived are 31–74 mm SL, and 29–46 mm SL for *C. kingsleyae* and *C. finleyi* respectively.

As in *Thysia*, the first *pelvic fin* ray is the longest, and is greatly produced in adult males. Unlike *Thysia*, there is no sexual dimorphism in the shape of the caudal fin margin which, in *Chromidotilapia*, ranges from subtruncate to gently rounded.

Coloration. As far as I can tell from the literature, especially the excellent colour photographs in Linke & Staeck (1981), all known species of *Chromidotilapia* have an unusual form of sexually dimorphic coloration. That is, an extensive metallic sheen, ranging from coppery to silver in colour, on the dorsal fin of sexually active females. Although a metallic band is developed on the dorsal fin of adult females in many *Pelvicachromis* species, it is, in these, far less extensive an area, and is a much more clearly defined band than is the case in *Chromidotilapia*. Again, judging from the literature, the *Chromidotilapia*-type of female dorsal fin colouring has not been recorded in other taxa of African cichlids, but our knowledge of live colours in these fishes is extremely limited. A possible exception, for example, may be *Nanochromis caudifasciatus* (see p. 174 for its new generic placement); in Linke & Staeck's (1981) figure of that species there is seemingly a silvery sheen on the female's dorsal fin which closely approximates to that of *Chromidotilapia* in area and appearance. In at least one species (*C. finleyi*, Trewavas, 1974) young fishes have a spot on the dorsal fin closely resembling a *Tilapia*-spot.

Breeding habits. Chromidotilapia is unique amongst the pelmatochromines in being a mouth-brooder. The breeding biology of *C. guntheri* is described in some detail by Myrberg (1965), there are general accounts of other species in Linke & Staeck (1981), and the mouth-brooding habits of *C. batesii* and *C. guntheri* are reviewed in the broad context of the cichlids as a whole by Peters & Berns (1978).

Included species. It is clear from the literature (Thys, 1968*a*; Trewavas, 1974 and personal communications; Linke & Staeck, 1981), that species level taxonomy for *Chromidotilapia* is in a very unsatisfactory state. Currently, seven nominal species are recognised, *viz.*: *C. kingsleyae* Blgr. 1898; *C. guntheri* (Sauvage), 1882, with two subspecies (see Trewavas, 1974), *C. batesii* (Blgr), 1901; *C. finleyi* Trewavas, 1974; *C. linkei*, Staeck, 1980; *C. schoutedeni* (Poll & Thys), 1967, and *C. busumtwensis* Paulo, 1979. It seems very likely from Linke & Staeck's (1981) account of supposedly intraspecific colour variation, that a number of sibling species probably have yet to be recognised and described.

Trewavas (cited by Linke & Staeck [1981:89] as a personal communication) has suggested that *Pelvicachromis humilis* (Blgr), 1916 may be closely related to, if not actually a member of, *Chromidotilapia*. Certainly the general facies of that species are distinctive amongst the other *Pelvicachromis*, and do resemble those of *Chromidotilapia*. However, *P. humilis* does not share with *Chromidotilapia* any of the critical autapomorphies defining that genus, but it does share with other *Pelvicachromis* species the apomorphic features of that taxon (see. p. 174).

PELVICACHROMIS Thys van den Audenaerde, 1968

TYPE SPECIES. *Pelmatochromis pulcher* Boulenger, 1901 (by original designation).

SYNONYMY. *Pelmatochromis* (part): Pellegrin, 1904 (the species *pulcher, subocellatus* and *taeniatus*); Boulenger, 1915 (the species *pulcher, kribensis, subocellatus* and *taeniatus*); Boulenger, 1916 (the species *humilis*); Regan, 1922 (as for Boulenger, 1915 and 1916).

Pelmatochromis (*Pelvicachromis*): Thys, 1968*a* (the species *pulcher, humilis, roloffi, subocellatus, taentiatus* [with which is synonymised *kribensis*], and a number of informally named taxa).

Like the other subgenera defined by Thys (1968*a*), *Pelvicachromis* was raised to generic rank by his referral (Thys, 1968*b*) of the nominate subgenus of *Pelmatochromis* to *Tilapia*, and by Trewavas' (1974) subsequent recognition of that subgenus as a full genus.

Thys (1968*a*) defined and diagnosed *Pelvicachromis* on a single feature, the unusual sexual dimorphism exhibited by the pelvic fins. In *Pelvicachromis* females the second or third branched pelvic ray is the longest, thereby giving the fin a distinctly rounded apex to its distal margin; in males, the first pelvic ray is clearly the longest and is often further produced in sexually active males.

Judging from extra- and intrafamilial out-group comparisons, this characteristic should be treated as an autapomorphy for the genus. However, it is closely approached by most, if not all

species of *Nanochromis* (*sensu* Thys, 1968*a*; but see below where the taxon is subdivided into two related genera). Pelvic fins in which the second and third rays are the longest also occur in at least one other African lineage, *Orthochromis* (Greenwood, 1979:297). In *Orthochromis*, however, this fin character is congruent with other apomorphies which would not indicate a close phyletic relationship with either *Pelvicachromis* or *Nanochromis*; furthermore, in *Orthochromis* the shape of the pelvic fins is identical in both sexes. As note above, in *Nanochromis*, as in *Pelvicachromis*, the fin is sexually dimorphic, but, unlike *Pelvicachromis*, *Nanochromis* females have the second ray only very slightly longer than the first; despite that, the apex of the fin's distal margin has a rounded rather than a pointed appearance. Again, there are congruent apomorphic features which indicate that *Nanochromis* is a distinct lineage.

At least as far as morphological features are concerned, the characteristic pelvic fin dimorphism of *Pelvicachromis* would seem to be the sole autapomorphic feature for the genus. That character, combined with the rather steeply decurved dorsal head profile, the short snout and the relatively elongate body-form in all species, make *Pelvicachromis* an easily recognisable member of the pelmatochromine group.

DIAGNOSIS. *Pelvicachromis* is distinguished from other genera of African cichlid fishes by the following characters taken in combination: Body form relatively elongate and moderately compressed, dorsal head profile decurved (Fig. 18).

Neurocranial apophysis for the upper pharyngeal bones usually of the *Tilapia*-type, that is formed from the parasphenoid only, but in at least some individuals of one species it is of the *Tropheus*-type, with small contributions from the basioccipital bones (see Greenwood, 1978). Supraoccipital crest relatively low, and not rising to a high peak posteriorly (Fig. 19). Supraethmoid and vomer in contact in at least two species. Palatine bone with a two-point neurocranial contact, anteriorly with an articulation in the region of the ethmovomerine suture, and posteriorly with a facet on the ventral face of the lateral ethmoid.

A visor-like, clearly circumscribed hanging pad anterior to the upper pharyngeal bones. Posterior facing margins of the major upper pharyngeal bones (the fused 3rd and 4th pharyngobranchials of each side) aligned so as to form a broad and shallow V with an anteriorly directed apex. No 'kukri'-shaped teeth (see p. 197) on the lower pharyngeal bone. Anterior blade of the lower pharyngeal bone short, contained 3–4 times in the overall length of the bone.

Infraorbital series of bones complete, the first infraorbital (lachrymal) usually with four openings to its laterosensory canal, but possibly in some species (or individuals) with five openings (see p. 171).

Outer row teeth in both jaws unicuspid and of the compressed-conical type (see p. 158), some teeth situated anterolaterally in the dentary have the cusp directed posteriorly and not buccally (Figs 8 & 9). Inner row teeth arranged in 1–3 rows, unicuspid or with weak and bilateral shoulders.

Lower jaw length less than 50 percent of head length. Premaxillary ascending processes as long as, slightly longer or slightly shorter than the alveolar arms. Anguloarticular with a roofed passage for the mandibulo-preopercular laterosensory canal. Mouth horizontal or very slightly inclined.

Scales cycloid. 25–30 in the lateral-line series; lateral-line clearly separated from the dorsal fin base over its entire length, by $1\frac{1}{2}$ or two scales at its highest point (above the 8th or 9th pored scales) and by one large and one very small scale above the last 4–6 pored scales. Cheek with 2 (rare) or 3 rows of scales; a small naked area anteroventrally sometimes present. Chest scales distinctly smaller than those on the belly and anteroventral aspects of the flanks, the size intergradation being rather abrupt. Sixteen scales around the caudal peduncle.

Gill-rakers of the outer row on the first ceratobranchial long, pachydermatous and crescentic, aligned transversely and close to the arch, the concave upper face variously tuberculate, the distal tip produced and horn-like; 9–12 in number. Epibranchial rakers of the first arch slender and flattened, sword- or dagger-shaped, arranged in a single row except near the epi-ceratobranchial junction. Microbranchiospines are absent.

Abdominal vertebrae 13–15 (mode 14) in number, caudal elements 10–12 (mode 12), giving total counts of 23–27 (all counts exclude the fused PU1 and U1 centra).

A single, well-developed supraneural (predorsal) bone. Dorsal fin with 14–16 spines, anal with 3.

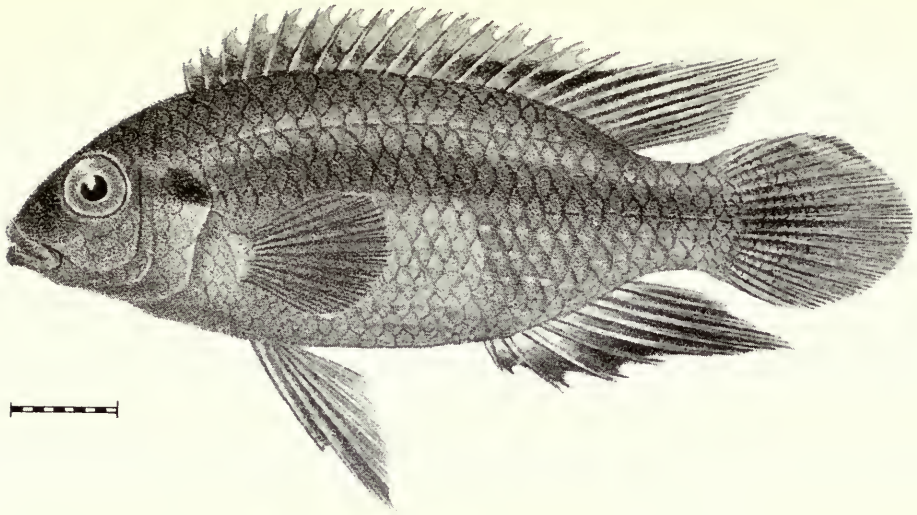

Fig. 18 *Pelvicachromis pulcher*, one of the types. From Boulenger (1901); *Proceedings of the Zoological Society of London*. Scale bar in mms.

Caudal fin rounded, but showing sexual dimorphism in some species where males have the median rays, or the lower rays of the upper lobe, produced. Pelvic fins sexually dimorphic; females with the second ray (sometimes both the 2nd and 3rd rays) longer than the first ray, thus producing a rounded apex to the fin's distal margin; in males the first ray is noticeably the longest, and the fin has a pointed apex.

Body coloration in breeding individuals with a marked sexual dimorphism. No true *Tilapia*-spot, but in some species the females have a dark spot approximately in the position of the *Tilapia*-spot.

Apparently all species are cave spawners and breeders.

NOTES ON THE ANATOMY AND OTHER FEATURES. In its overall morphology, the *neurocranium* in *Pelvicachromis pulcher, P. subocellatus* and *P. taeniatus* (the only species for which adequate study material was available) closely approximates to that of *Pelmatochromis buettikoferi* (cf. Figs 3 & 19). The supraoccipital crest, however, is much lower and slopes gently rather than steeply. The fronto-parietal crests in the *Pelvicachromis* species examined are better developed than in *P. buettikoferi*, and unlike that species, the vomer and supraethmoid are suturally united in *Pelvicachromis*, which thus shows the common African cichlid condition. In both genera the ethmovomerine region of the skull is short (*ca.* $3\frac{1}{4}$–$3\frac{1}{2}$ times in neurocranial length) and slopes upwards fairly steeply at an angle of about 50° to the horizontal.

The available neurocrania of *Pelvicachromis pulcher* and *P. taeniatus* have a typical *Tilapia*-type apophysis for the upper pharyngeal bones, but in the single *P. subocellatus* examined there is, bilaterally, a very small contribution by the basioccipital, the apophysis thus closely resembling the *Tropheus*-type (Greenwood, 1978).

In all three species the lateral commissure is of the *Haplochromis*-type, and a well-developed precommissural bridge is present in *P. pulcher* and *P. subocellatus*, but is absent in *P. taeniatus*, as are any indications of precommissural spurs on the prootic (see Greenwood, 1986).

The *infraorbital bone series* is complete (Fig. 5D). The first bone (lachrymal) has four openings to its laterosensory canal system; almost half of the second bone overlaps the posteriorly directed flange on the lachrymal. Trewavas (1983) records that some (but unnamed) *Pelvicachromis* species are variable with respect to the number of openings in the lachrymal laterosensory canal system,

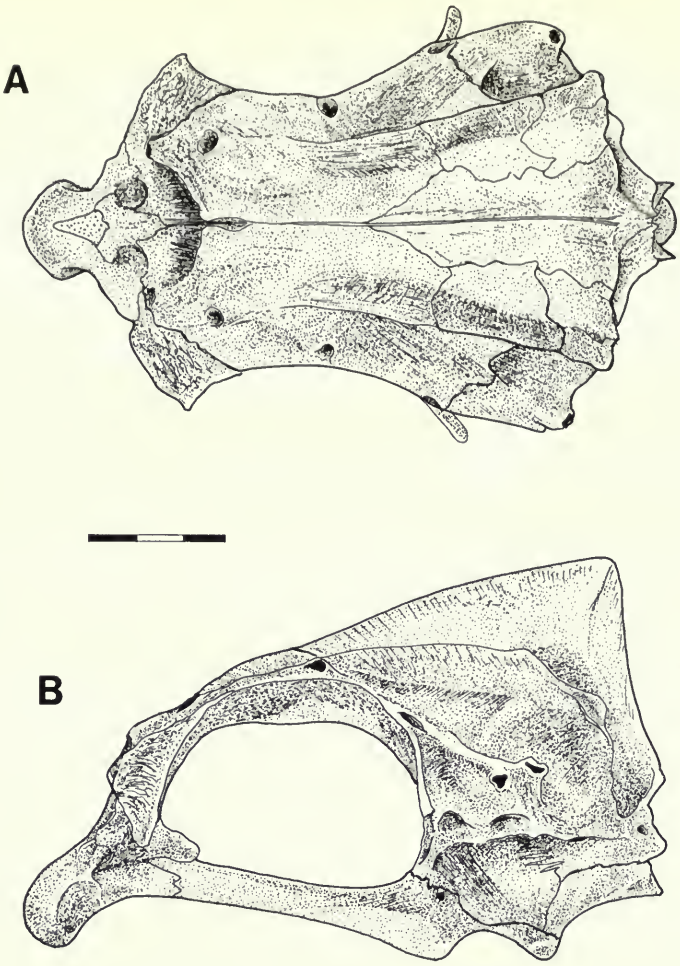

Fig. 19 Neurocranium of *Pelvicachromis pulcher* in: A. Dorsal, and B. Left lateral view; the basisphenoid bone is missing in this specimen. Scale bar in mms (BMNH 1901.1.28:13–20).

having either 4 or 5; that situation was not encountered in any of the species or specimens I examined.

The *vertebral column* is composed of 23–26 vertebrae (excluding the fused PU1 and U1 centra), comprising 13 or 14 (mode) abdominal and 10–12 (mode) caudal elements (figures obtained from radiographs of four species, viz: *P. pulcher* type series; *P. taeniatus* holotype and one other specimen, and specimens identified as *P. subocellatus* and *P. roloffi*). Counts were also obtained from radiographs of *P. humilis* holotype, and are noticeable for the higher number (15) of abdominal centra (total count 27); the taxonomic status of *P. humilis* is discussed later (p. 174).

A single supraneural (predorsal) bone is present in all the species and specimens radiographed.

In *other osteological features* examined the skeleton of *Pelvicachromis* showed no seemingly significant differences from that of the other pelmatochromines considered so far. The *pharyngobranchial skeleton*, for example, is like that in *Pelmatochromis*, as is the lay-out of its pharyngeal bones. There is an expansive cartilaginous projection from the anterior margin of the second epibranchial bone (as in *Pelmatochromis*), although the shank ridge on the fourth epibranchial is better defined and spine-like in *Pelvicachromis* (see p. 151). The lower pharyngeal bone and its dentition are similar in both genera (see Fig. 6).

The *gill-rakers* show some interspecific variation in the extent to which the upper surface is tuberculated, and in the extent to which the median membrane is developed between the inner and outer raker series on the first ceratobranchial. However, possible differences in the quality of preservation (and the length of time in preservative) render difficult any assessment of the significance that can be attached to these differences. Be that as it may, the rakers in all the species examined are clearly of the derived pelmatochromine type discussed on p. 159.

Myology and arthrology. Only *P. pulcher, P. subocellatus* and *P. roloffi* have been dissected. In none does the myology or the arthrology of the jaws show any outstanding features. Both are essentially of the type described for *Pelmatochromis* (p. 153), except that, as in most African species dissected, there is no fusion between the tendons A1β and Aw in the *adductor mandibulae* series.

Likewise, the dorsal pharyngobranchial musculature is like that of *Pelmatochromis*, and is thus of the basic cichlid type. Ventrally, and unlike the other pelmatochromines discussed so far, the *obliquus ventralis* 3 muscle in *P. pulcher* and *P. subocellatus* has no insertion on the semicircular ligament, but inserts entirely on the third hypobranchial. *Pelvicachromis roloffi*, on the other hand, has a few fibres of the muscle attaching to the ligament, as is the case in the other pelmatochromines.

All three species have the typical African cichlid condition of the *transversus ventralis anterior* muscle being interrupted medially by the anterior blade of the lower pharyngeal bone (see Stiassny, 1982).

Squamation. Little need be added to the details given in the diagnosis (p. 170), except to note that there are few scales between the highest point of the upper lateral-line and the dorsal fin base, namely $1\frac{1}{2}$ or 2, and a single scale, or one large and one very small scale, between the fin base and the last 4–6 pored upper lateral-line scales.

Chest scales in *Pelvicachromis* are distinctly smaller than those on the belly and anteroventral aspects of the flanks, and there is a fairly abrupt change in size between these scales and those on the chest. The degree of abruptness shows some interspecific variation.

Fins. The nature of the sexual dimorphism in the pelvic fins was noted above (p. 169), where the differences between *Pelvicachromis* and members of the *Nanochromis* group (*sensu* Thys, 1968*a*) were also discussed. The phyletic significance of those similarities, and differences, will be considered later (p. 194).

As Thys (1968*a*:357;399) noted, there are two distinct but sympatric groups of *Pelvicachromis* species. In one there is an obvious sexual dimorphism in caudal fin shape, with males having the central caudal fin rays (or the lower few rays in the upper lobe of the fin) somewhat extended so as to disrupt the outline of an otherwise rounded-subtruncate to clearly rounded margin (the latter being the usual female condition). The second group shows no sexual dimorphism in caudal fin outline, which is either rounded or rounded-subtruncate in both sexes.

Dentition. In the *Pelvicachromis* species I have examined, the dentition is typically that of all group II pelmatochromine taxa (see p. 158). It has proved impossible to determine at what size the anterolateral, backward-pointing teeth appear in the dentary, or to gather any information on the nature of the teeth in small specimens.

Inner row teeth of both jaws are always slender and somewhat smaller than those of the outer row, and show a variety of crown shapes; some have simple attenuated-conical crowns, others are very similar to the compressed-conical teeth of the outer row, or may have compressed-conical crowns with faint traces of shoulders flanking the tip bilaterally. Again, because of insufficient material covering small specimens, it is impossible to tell if there are size correlated changes in the nature of the inner teeth.

Coloration. A true *Tilapia*-spot has not been recorded in any *Pelvicachromis* species, and it has yet to be discovered whether or not the similarly placed ocellus (or conjoined ocelli) which occur in the adult females of some species is the homologue of a *Tilapia*-spot (see colour figures, pages 91, 115 & 118 in Linke & Staeck, 1981).

Breeding. All the species whose breeding behaviour is known are substrate spawners and guarders, often using holes and small cave-like irregularities of the bottom (Linke & Staeck, 1981: 82–87). Aquarist literature relating to this genus can be misleading since there are considerable difficulties involved in species identification, and because several 'trade' binomia have been con-

cocted by dealers (see Thys, 1968*a*). However, the accounts given by Linke & Staeck (1981) are both critical and carefully researched, and provide a good summary of *Pelvicachromis* breeding biology.

Included species. Species level taxonomy for *Pelvicachromis* is in a far from satisfactory state, as Thys (1968*a*) clearly showed in his critical review of the genus. Currently, *P. pulcher* (Blgr) 1901, *P. humilis* (Blgr) 1916, *P. roloffi* (Thys) 1968, *P. taeniatus* (Blgr) 1901 and *P. subocellatus* (Gnthr) 1871 are recognised, together with a number of informally designated 'forms' discussed by Thys (1968*a*), and by Linke & Staeck (1981); for detailed synonymies of these species reference should be made to both those publications.

Uncertainties about the correct generic placement of *Pelvicachromis humilis* were noted above (p. 169) in connection with Trewavas' suggestion (pers. comm., mentioned by Linke & Staeck, 1981) that the species could be a member of the *Chromidotilapia* lineage.

Certainly in its general facies *P. humilis* does approach the *Chromidotilapia* type, particularly in having a straight and sloping dorsal head profile rather than a rounded, decurved one. It also differs in certain osteological characters from the modal *Pelvicachromis* condition; the supra-occipital crest is lower, the ethmovomerine skull region is slightly longer and slopes at a somewhat lower angle (*ca.* 40° cf. 50° to the horizontal), the interorbital region is narrower, and the vertebral count (27) is higher as a consequence of there being 15 rather than 13 or 14 abdominal centra.

However, in other antatomical and osteological features, *P. humilis* shows nothing which would suggest that it is more closely related to *Chromidotilapia* than to *Pelvicachromis*.

Since *P. humilis* apparently shares none of the autapomorphic features characterising *Chromidotilapia* (it is not, for instance, a mouth-brooder), it would seem best to treat it, for the time being, as a somewhat atypical member of the genus *Pelvicachromis*. Its relationships within that genus may be clarified when a detailed and wide-ranging species-level revision of *Pelvicachromis* has been carried out.

Parenthetically, note can be made of what seems to be an individual aberrancy in one of the two *P. humilis* specimens I have dissected. In that fish, besides the *adductor mandibulae* 1 muscle having a tendon to the maxilla, and its ventrally directed A1β tendon to the lower jaw, there is a third and short tendon linking the head of the muscle with the coronoid process of the anguloarticular bone (Fig. 20). The second specimen examined has the usual two-tendon arrangement.

PARANANOCHROMIS gen. nov.

TYPE SPECIES: *Pelmatochromis longirostris* Boulenger, 1903.

SYNONYMY. *Pelmatochromis* (part): Pellegrin, 1904 (the speices *longirostris* only); Boulenger, 1915 (the species *longirostris* and *caudifasciatus*).
Pelmatochromis (*Nanochromis*) in part: Thys, 1968*a* (the species *longirostris* and *caudifasciatus*)
Nanochromis (part): Trewavas, 1975 (the species *gabonicus*)

Thys (1968*a*:379–381) included *Pelmatochromis longirostris* and *P. caudifasciatus* in his subgenus *Nanochromis* (a taxon originally described and ranked as a genus by Pellegrin, 1904). Thys' reasons for so placing these two species was that, unlike most of the other pelmatochromines he dealt with, but like the species he referred to *Nanochromis*, both *P. longirostris* and *P. caudifasciatus* have only 12 (and not 16) scales around the caudal peduncle. He also expressed the belief that these two species, together with certain unnamed material '. . . seem to constitute a continuous evolutionary line' with *Nanochromis nudiceps* (the type species of Pellegrin's genus).

At the time Thys' paper was published (1968), *Nanochromis* (*sensu* Pellegrin) was rather poorly defined, the chief character given to distinguish it from *Pelmatochromis* (*sensu* Regan, 1922) being the extreme dorsad position of the upper lateral-line; Regan (*op.cit.*) diagnosed the genus on the basis of its having the 'Upper lateral line contiguous to dorsal fin', a slightly inaccurate description since almost the anterior half of that line is separated from the dorsal fin base by at least 1 scale row.

Thys (1968*a*) expressed doubts about the validity of the lateral line position as '. . . a good generic character' but did not elaborate further on that point, nor on what a 'good' generic character might be. He also expressed some misgivings about the significance of the reduced circumpeduncular

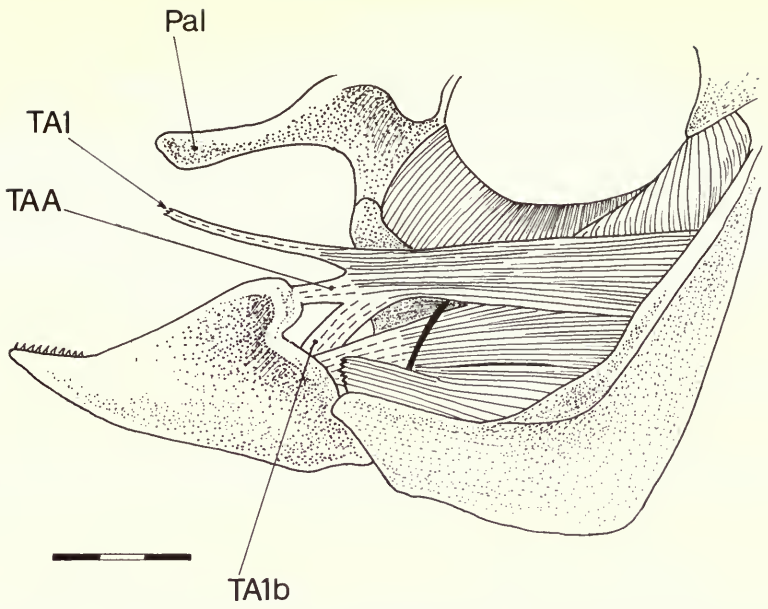

Fig. 20 An unusual arrangement of the tendons associated with the *adductor mandibulae* 1 muscle in an aberrant specimen of *Pelvicachromis humilis* (BMNH 1972.3.16:8–10). Left lateral view. Scale bar in mms. Pal = palatine bone; TA1 = maxillary tendon of the first adductor muscle; TAA = anomalous tendon inserting on the anguloarticular bone; TA1b = tendon from first adductor muscle to the lower jaw.

scale count since, although uncommon amongst African cichlids (where 16 scales are usual), it does occur in a few other species which, because of this feature, he had not assigned to a particular genus or subgenus.

Nevertheless, and presumably because *caudifasciatus* and *longirostris* fell into what he considered 'a continuous evolutionary line', Thys included the two species, with those of *Nanochromis*, as a distinct subdivision (i.e. subgenus) of *Pelmatochromis*.

In a phylogenetic context, I cannot agree with Thys on the supposed insignificance of the lateral-line position in *Nanochromis* (see p. 183), the more so since in that genus (*sensu* Pellegrin) it is congruent with other apomorphic features recently noted by Stewart and Roberts (1984). In my view, the partial but extreme contiguity of the dorsal fin base and the upper lateral-line, together with the other synapomorphic features in *Nanochromis* (especially the nature of the infraorbital bone series; see p. 181) indicate an *immediate* common ancestor for the species showing them. That ancestor was not shared by *longirostris* and *caudifasciatus* (or by the species *gabonicus* of Trewavas, 1975; see synonymy above), all taxa in which the *Nanochromis* synapomorphies are not present.

However, *Parananochromis* (which I have erected for the three latter species) and *Nanochromis* (*sensu* Pellegrin) do share, uniquely amongst the pelmatochromines, two apomorphic characters, namely 12 scales around the caudal peduncle, and a *Haplochromis*-type neurocranial apophysis for the upper pharyngeal bones (the latter a feature not noticed by Regan [1922], Thys [1968*a*], or Trewavas [1975]).

On the basis of those synapomorphies I would postulate a more distant, but still close, common ancestry for the two genera. It might be argued that the relationship of the lineages could best be indicated by ranking them as subgenera of *Nanochromis*. I would agree with that argument but for the possibility of future research showing the existence of two lineages within *Nanochromis* as presently construed (see p. 187). For that reason I prefer to treat *Parananochromis* as a genus, and rely on a cladogram (Fig. 29) to show its sister-group relationship with *Nanochromis*. In the sense that *Nanochromis* and *Parananochromis* are sister taxa, I would agree with Thys' idea that together

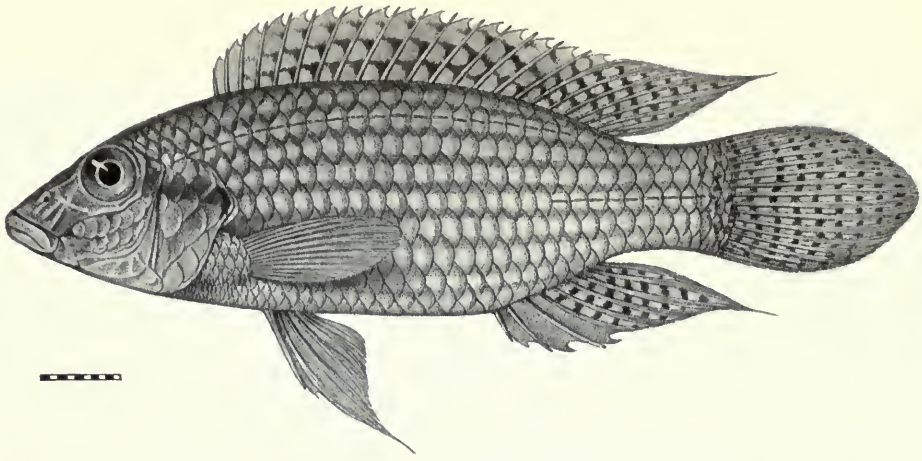

Fig. 21 *Parananochromis longirostris*; holotype. From the original drawing by J. Green. Scale bar in mms.

they form a continuous evolutionary line, with *Nanochromis* representing the more derived portion of the lineage.

Thys (1968*a*) notes that in the species he referred to his subgenus *Nanochromis* there is '. . . a feebly developed or even no hanging pad in the roof of the pharynx' and that the ventral fins are rounded in both sexes. The species which I have examined, and which I place in *Parananochromis*, all have, *pace* Thys, a well-developed and typically circumscribed, visor-like hanging pad, and although the pelvic fins are distinctly or almost rounded in females, they are pointed in males.

Thys & Loiselle (1971) described two new *Nanochromis* species (*sensu* Thys, 1968*a*), *N. robertsi* and *N. cavalliensis*. Superficially, both seemingly would belong to *Parananochromis* since neither shows the defining features of *Nanochromis* (*sensu* Pellegrin, see p. 181). However, in both species the neurocranial apophysis for the upper pharyngeal bones is of the *Tilapia*-type, and both have 13 or 14 scales around the caudal peduncle (cf. 12 in *Parananochromis* and *Nanochromis*, and 16 in other group II pelmatochromines). On those grounds I exclude *robertsi* and *cavalliensis* from both *Parananochromis* and *Nanochromis* (see p. 188).

DIAGNOSIS. *Parananochromis* is distinguished from other genera of African cichlids by the following characters taken in combination: Body form moderately elongate and compressed; dorsal head profile sloping steeply but somewhat decurved (Fig. 21).

Neurocranial apophysis for the upper pharyngeal bones of the *Haplochromis*-type, with substantial contributions from the basioccipital. Supraethmoid not contacting the vomer in the one species examined (*P. longirostris*). Supraoccipital crest relatively low, and not rising to a high peak posteriorly. Palatine with a two-point neurocranial contact, anteriorly through an articulation in the region of the ethmovomerine suture, and posteriorly with the ventral face of the lateral ethmoid (see Greenwood, 1985*a*). A calyx is developed between the metapterygoid and the hyomandibula.

Infraorbital bone series complete, the first infraorbital (lachrymal) with four openings to its laterosensory canal (Fig. 5C).

Lower jaw length less than 50 percent of the head length; anguloarticular with a roofed canal for the passage of the mandibulo-preopercular laterosensory canal.

Outer row jaw teeth of the typical group II pelmatochromine type (see p. 158); inner row teeth unicuspid, arranged in from 1–3 rows.

A well-developed and clearly circumscribed, visor-like hanging pad developed from the pharyngeal roof immediately anterior to the upper pharyngeal bones. Posterior facing margins of the fused 3rd and 4th pharyngobranchials aligned so as to form a broad and shallow V, its apex

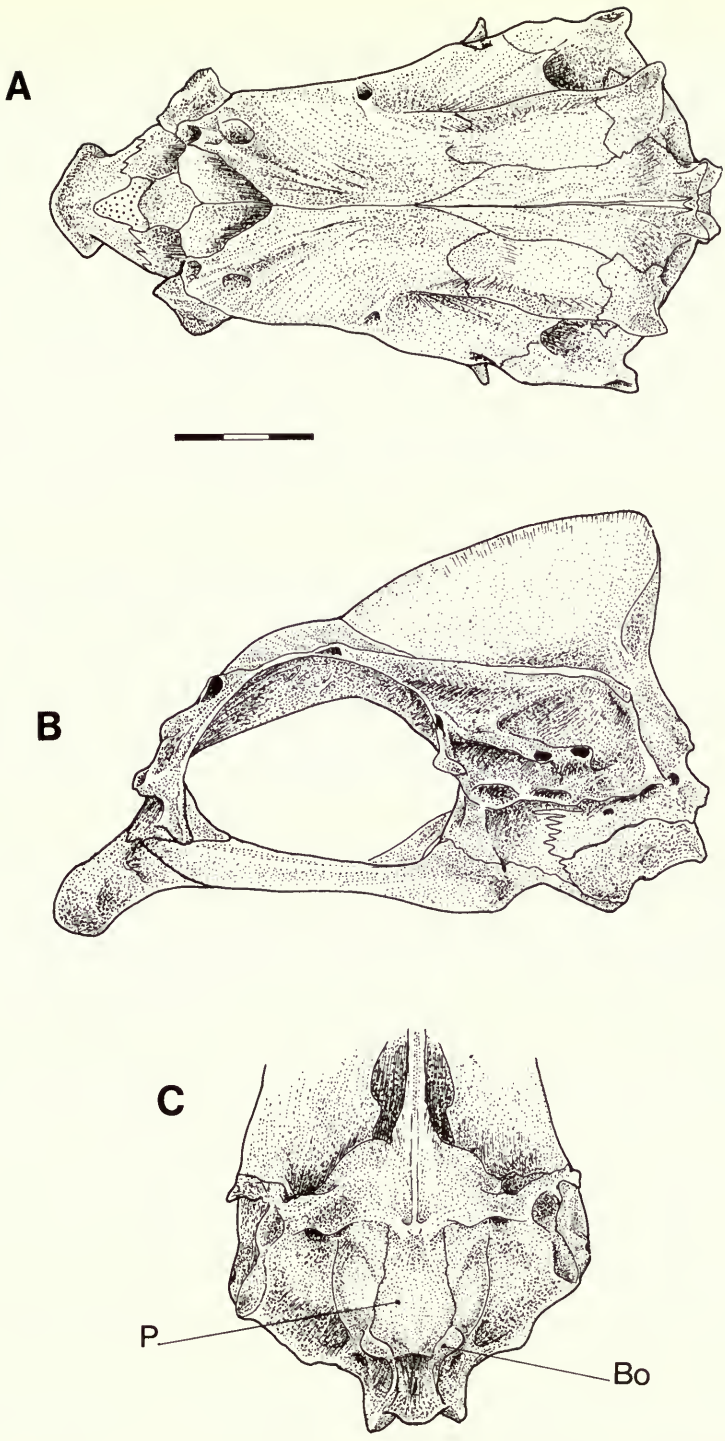

Fig. 22 Neurocranium of *Parananochromis longirostris* in A. Dorsal; B. Left lateral view. C. Neurocranial apophysis for the upper pharyngeal bones. Scale bar in mms. P = parasphenoid; Bo = basioccipital (BMNH 1903.7.28:77–83; one of the syntypes).

directed anteriorly (Fig. 4A). Anterior blade $3\frac{1}{2}$–4 times in the overall length of the bone. No 'kukri'-shaped teeth on the lower pharyngeal bone (see p. 197).

Scales cycloid. Lateral-line with 27–30 scales; upper lateral-line separated at its highest point (*ca.* the 8th pored scale) from the dorsal fin base by $1\frac{1}{2}$ scales, and by one scale over the last 3–5 pored scales. Chest scales noticeably smaller than those on the belly and anteroventral aspects of the flanks, the size transition between these scales and those of the chest abrupt. The two or three median rows of scales on the chest are larger than those situated more laterally. There are 12 scales around the caudal peduncle.

Gill-rakers in the outer row of the first gill-arch of the typical group II pelmatochromine type (see p. 160). Microbranchiospines absent.

Vertebral column with 12–14 abdominal and 12–13 caudal elements (excluding the fused PU1 and U1 centra), giving a total count of 25 or 26. A well-developed supraneural (predorsal) bone present.

Caudal fin with slight sexual dimorphism in at least one species where the lower 3 or 4 rays in the upper lobe are produced; otherwise the caudal fin margin is slightly subtruncate to rounded in both sexes. Pelvic fins with the first ray produced in males, the second ray as long as or but slightly shorter than the first in females. Dorsal fin with 14–16 spines, anal with 3.

Apparently some sexual dimorphism in body coloration; at least one species (*P. caudifasciatus*) with a fairly extensive silvery sheen on the dorsal fin in sexually active females. No *Tilapia*-spot, or any markings resembling one, is developed.

In other features (as in many of those listed) *Parananochromis* resembles *Pelvicachromis*.

NOTES ON THE ANATOMY AND OTHER FEATURES. A shortage of material for deep dissections or for making osteological preparations has restricted the number of observations which can be made on the anatomy of *Parananochromis*; radiographs, however, are available for all three species.

The *neurocranium* in *P. longirostris* closely resembles that of *Pelvicachromis pulcher* (cf. Figs 22 & 19), except that the supraoccipital crest is, relatively, a little higher in the former species. The crest has a gently curved dorsal margin so that, as in *Pelvicachromis pulcher*, there is no obvious posterior peak; the anterior tip of the supraoccipital lies above the midpoint of the orbit. The length of the ethmovomerine region is contained about $3\frac{1}{2}$ times in the neurocranial length, and slopes at an angle of about 65° to the horizontal.

Unlike *Pelvicachromis pulcher*, the pharyngeal apophysis in all three *Parananochromis* species is of the typical *Haplochromis*-type, with clearly demarcated and moderately large basioccipital facets. Thys (1968*a*) makes no comments on the nature of this apophysis in either *P. longirostris* or *P. caudifasciatus*. Trewavas (1975:233), referring to *P. gabonicus*, notes that '. . . although the base of the skull was not examined in this unique specimen, the other characters indicate that it belongs to the group in which the apophysis . . . is formed by the parasphenoid alone'. Presumably she was influenced, in making that remark, by her considering the species to be a *Nanochromis* (*sensu* Pellegrin), a genus which Regan (1922) placed in his division of cichlids having a *Tilapia*-type apophysis. I have examined the apophysis in Trewavas' specimen of *gabonicus*, and find that, in fact, it is of the typical *Haplochromis*-type. Stewart & Roberts (1984) were the first to record, but without further comment, that the apophysis in at least some true *Nanochromis* species is of the *Haplochromis*- and not the *Tilapia*-type. I have now been able to examine that apophysis in all described species of *Nanochromis*, and can confirm that in each it is of the *Haplochromis*-type.

The lateral commissure in *Parananochromis longirostris* is of the *Haplochromis*-type (Greenwood, 1986) and a precommissural bridge is present.

As far as can be told from radiographs, the shape of the neurocranium in *Parananochromis caudifasciatus* is like that of *P. longirostris*, but that of *P. gabonicus* has a lower supraoccipital crest, probably lower even than in species of *Pelvicachromis*.

The *infraorbital series* in all three species is complete (cf. that in *Nanochromis*; see p. 186), and the first infraorbital bone (lachrymal) has four openings to its laterosensory canal; in *P. longirostris*, the only species checked, about half of the second infraorbital overlaps the posteriorly directed flange of the lachrymal (Fig. 5C).

The *vertebral column* is composed of 25 or 26 vertebrae, comprising 12–14 abdominal and 12 or 13 caudal elements (the fused PU1 and U1 centra excluded). A single well-developed supraneural

(predorsal) bone is present (it is absent or greatly reduced in size amongst species of *Nanochromis*, see p. 187).

Gill-rakers on the cerato- and epibranchial of the first gill-arch are like those described for *Chromidotilapia* (see p. 160). There is, apparently, some interspecific variability in the extent to which the median membrane between the inner and outer rows of gill-rakers is developed. The membrane in *P. longirostris* is very low and barely produced into a tubercle between each pair of inner and outer rakers, whereas in *P. caudifasciatus* and *P. gabonicus* it is high, with prominent tubercles; in the latter species the tip of each outer-row raker on the ceratobranchial is noticeably produced and horn-like.

The *pharyngobranchial skeleton*, except for the pharyngeal bones, has been examined only in *P. longirostris*. In all three species the *lower pharyngeal bone* has a deep median indentation of its posterior margin and a short anterior blade (its length contained *ca.* $3\frac{1}{2}$ to 4 times in the overall length of the bone), features which impart a distinctly arrow-head outline to the bone. The lower pharyngeal teeth are somewhat widely spaced, few in number, and the outermost row is implanted very close to the margin of the bone.

The *upper pharyngeal bones* are subovoid in outline and, as in all other pelmatochromines (and the majority of African cichlids), are orientated so that their posteriorly directed margins form a broad and shallow V whose apex points anteriorly (see Fig. 4A).

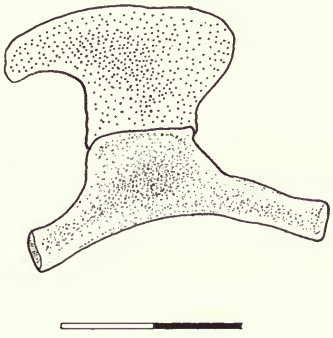

Fig. 23 Right epibranchial 2 of *Parananochromis longirostris* in dorsal view, to show the extensive cartilaginous flange (coarsely stippled) associated with its anterior border. Scale bar in mms. (BMNH 1903.7.28:77–83; one of the syntypes).

In *P. longirostris*, the only species dissected in depth, there is a very expansive, anvil-shaped cartilage developed on the anterior margin of the second epibranchial (Fig. 23); it almost fills the anterior part of the hanging pad, and extends to its anterior border.

Squamation. An unusual feature of *Parananochromis*, one which I would consider a possible synapomorphy for the lineage (but see p. 190), is the presence on the chest of 3 or 4 median rows of relatively but distinctly larger scales within the otherwise small scales of this area. The size transition between the small chest scales, and those on the ventrolateral aspects of the flanks and belly is abrupt.

Also characteristic of *Parananochromis*, but a feature shared with *Nanochromis*, is the reduced number (12) of circumpeduncular scales.

Cheek squamation patterns are interspecifically variable. In *P. gabonicus* there are two rows, with a deep naked strip ventral to the second row, and an extensive naked area anteroventrally; *P. caudifasciatus* has a large anteroventral naked area, but otherwise the cheek is covered by 3 or 4 rows of scales; *P. longirostris* has 2 or 3 scale rows, with a naked strip (about one scale row deep) along its entire ventral margin, and a large naked area anteroventrally.

The upper lateral-line is high on the body, with $1\frac{1}{2}$ scales separating it from the dorsal fin base at

its highest point (about the 8th or 9th pored scale), and one scale separating the fin base from the last 4 or 5 pored scales.

The scales on the nape and nuchal region are not noticeably reduced in size (cf. *Nanochromis*; p. 183).

Fins. Only an adult female of *P. gabonicus* is available, but in the other two species adult males have the first branched pelvic ray clearly longer than the second. In the female *P. gabonicus* the second ray is as long as the first, and in female *P. longirostris* and *P. caudifasciatus* the second ray is either as long as the first or is but marginally shorter, and consequently the apex of the fin is more nearly rounded than pointed.

The margin of the caudal fin is rounded to subtruncate in females of all three species, and, apparently, also in adult male *P. caudifasciatus*. Sexually active males of *P. longirostris*, however, have the margin of the upper caudal lobe, at about its mid-section, produced into a short, broadly triangular projection (see figure in Linke & Staeck, 1981:66). Judging from the figure of *P. gabonicus* in that publication (*op.cit.*:65), there is a slight indentation at about the mid-point of the posterior margin, but I have not been able to confirm this from preserved specimens.

Dentition. None of the three specimens has any particular character of note in its dentition, which is typically that of a group II pelmatochromine (see p. 158). Since only one small specimen is available (a 21 mm SL *P. caudifasciatus*) it is not possible to make any generalisations about possible ontogenetic changes in tooth form. In this small fish the outer teeth are unicuspid, but some teeth have faint traces of a shoulder below the major cusp; the crowns are but weakly curved, and no teeth with posteriorly directed crowns are present in the dentary. No inner row teeth are visible, even at a magnification of 30X.

Myology and arthrology of the jaws and gill-arches. Only *P. longirostris* has been dissected, and no outstanding features were noted in the musculature of the jaws.

In the dorsal pharyngobranchial musculature no part of the *levator posterior* muscle inserts on the horn of the lower pharyngeal bone. Except for a small tendinous slip inserting on the 4th epibranchial bone, all of the *levator externus* 4 muscle inserts on that horn. This condition is more like that in *Thysia* (see p. 163) than that in the other pelmatochromines. In those, a small part of the *levator posterior* inserts on the horn, and the insertion of the *levator externus* 4 on the epibranchial is musculose rather than tendinous.

In its ventral branchial musculature, *Parananochromis longirostris* is like the majority of pelmatochromines (and probably the other African cichlids; see Greenwood, 1985*a*:163) since a large part of the *obliquus ventralis* 3 muscle inserts on the semicircular ligament (*Pelvicachromis* is unusual in this respect, because in two of the three species dissected the muscle inserts entirely on the third hypobranchial bone; see p. 173).

Coloration. No information is available on the live colours of *P. gabonicus* (see Trewavas, 1975 for the preserved coloration of a female fish), and for *P. longirostris* the data are from a recently dead male (see Linke & Staeck, 1981:66). There is obvious sexual dimorphism in the coloration of *P. caudifasciatus* (see Linke & Staeck, 1981:58–59), although this may be less pronounced than in other pelmatochromines; these authors record a shiny, metallic band on the spinous dorsal fin of sexually active females (see p. 169).

Breeding biology. No information is available for either *P. gabonicus* or *P. longirostris*, but *P. caudifasciatus* is known to be a substrate spawner (Linke & Staeck, 1981:60).

Included species. At present only three named species can be referred to *Parananochromis*; that is *P. longirostris* (Blgr) 1903, *P. caudifasciatus* (Blgr) 1913 and *P. gabonicus* (Trewavas) 1975. Judging from Thys' (1968*a*) comments, however, more species will doubtless be added.

Two species, *Nanochromis robertsi* and *N. cavalliensis*, both described by Thys & Loiselle (1971) have a close superficial resemblance to the species of *Parananochromis*, but on other and derived characters appear to belong to a lineage distinct from both *Nanochromis* and *Parananochromis* (see p. 188).

NANOCHROMIS Pellegrin, 1904.

TYPE SPECIES: *Pseudoplesiops nudiceps* Blgr, 1899 (by original designation).

SYNONYMY. *Pseudoplesiops* (*non* Bleeker): Boulenger, 1899 (the species *nudiceps* and *squamiceps*).

Nanochromis: Pellegrin, 1904, replacement name for *Pseudoplesiops* Blgr, 1899 (the species *nudiceps* and *dimidiatus*); Boulenger, 1915 (the species *nudiceps, dimidiatus* and *squamiceps*); Regan, 1922 (none listed); Stewart & Roberts, 1984 (the species *nudiceps, dimidiatus, squamiceps, transvestitus, consortius, parilius, minor* and *splendens*).

Pelmatochromis (*Nanochromis*), in part: Thys, 1968*a* (the species *nudiceps, dimidiatus* and *squamiceps*).

Since its original description (under the preoccupied name *Pseudoplesiops*) the genus has been defined and diagnosed principally on the high position of its upper lateral-line. In all but two species a little more than the posterior half of the upper lateral-line is contiguous with the base of the dorsal fin, and fewer than five scales anterior to the point of contiguity are separated from the fin base by more than one, or one and a half, often very small scales.

The exceptional species, *N. dimidiatus* and *N. squamiceps*, have only the last 3 to 5 scales of the upper lateral-line contiguous with the fin base, the greater part of the line having one very small scale interposed between it and the fin base. The supposed distinctness of these two species has been queried by Matthes (1964); however, in Thys' opinion (1968*a*:307) they are not only distinct but may not even be closely related.

The inclusion of *dimidiatus* and *squamiceps* in *Nanochromis* rather than in *Parananochromis* (see above, p. 176) is based on their having an interrupted infraorbital bone series in which only the lachrymal and one other canal bearing bone is present, the latter not curving around, and closing, the posterior margin of the orbit (see below).

Pellegrin (1904), when proposing the new name *Nanochromis* for the taxon (see synonymy), noted the presence of a clearly defined hanging pad in the pharynx, and was the first author to comment on the close similarity between *Nanochromis* and *Pelmatochromis* (then conceived in its broadest sense [see Introduction] but probably used by Pellegrin with particular regard to the species now placed in the genus *Pelvicachromis*). Regan (1922), too, commented on *Nanochromis* being 'Scarcely different from *Pelmatochromis*'. Neither author, however, gave any reasons for their views.

Thys (1968*a*:380) broadened the earlier concept of *Nanochromis* to include certain species here referred to the new genus *Parananochromis*, but reduced the status of *Nanochromis* to a subgenus of *Pelmatochromis*. His definition of *Pelmatochromis* (*Nanochromis*) was based, principally, on all its constituent species having a reduced number of scales (12) around the caudal peduncle since he expressed doubts about the significance of the high lateral-line position as a group character. In my view (p. 194) the high lateral-line is a good apomorphy indicating the monophyletic nature of the species possessing it, and also serves as one of the synapomorphic characters defining the taxon *Nanochromis*. The first really detailed taxonomic account of *Nanochromis* is Stewart & Roberts' (1984) paper, a follow-up of their earlier work describing a number of new species from the Zaire River (Roberts & Stewart, 1976). Although I would question some of the supposed autapomorphies used by Stewart & Roberts (1984) to establish the monophyly of *Nanochromis*, the other characters used by them appear to be good, and synapomorphic, features for that purpose (see discussion below).

That *Nanochromis* is a member of the group II pelmatochromine lineage is established by the nature of the dentition, the morphology of its gill-rakers, and by the well-developed, visor-like pharyngeal hanging pad.

Before presenting a diagnosis for *Nanochromis* some consideration must be given to the four supposed synapomorphic features which, in addition to the high upper lateral-line position, Stewart & Roberts (1984:82–83) used to establish the monophyly of the genus. These characters, and comments upon them, are:

(1) Only two infraorbital bones, a lachrymal with two lateralis canals extending to the lower rim and an elongate second infraorbital that projects posteriorly rather than follows the orbital rim; the infraorbital lateralis canal terminates posteriorly at a pore on the cheek.

Reduced and, or, variously interrupted infraorbital series occur in at least three other African cichlid taxa, *viz. Lamprologus* (*sensu lato*; see Colombe & Allgayer, 1985), *Telmatochromis* and *Julidochromis*. None of these, however, has the characteristic lachrymal plus one elongate, handle-like bone seen in *Nanochromis*, and all have various apomorphic features which are not shared with *Nanochromis*. Furthermore, none shares with *Nanochromis* the visor-like hanging pad and peculiar

dental features of a group II pelmatochromine (see p. 157), or the high-positioned upper lateral-line of that genus.

The nature of the infraorbital series in *Nanochromis* would therefore seem to be an autapomorphy. Stewart & Roberts' statement about the number of openings to the lachrymal latero-sensory canal could, at first sight, be misleading since there are four openings on that bone, the plesiomorphic condition in cichlids. Presumably the authors exclude from their count the anterior and posterior openings (which are shown in fig. 3 of Stewart & Roberts, 1984) since these could be interpreted as not reaching the bone's lower (i.e. ventral) rim.

The elongate second infraorbital in *N. squamiceps* and *N. dimidiatus*, unlike that in the other species, does follow the curvature of the eye, and thus does not project straight posteriorly in a handle-like fashion. However, as in the other species, the infraorbital bones in *N. squamiceps* and *N. dimidiatus* do not form a complete bony rim to the orbit, and the infraorbital canal (or at least its lower portion) terminates posteriorly as a pore on the cheek. Interestingly, both these species, as will become apparent below, tend not to show certain '*Nanochromis*' characteristics in the fully-developed manner seen in the remaining species.

(2) No predorsal bones.

The absence of predorsal bones (supraneurals) is a derived feature in cichlids, where one bone is the usual condition and two are found amongst African cichlids only in such plesiomorphic taxa as *Heterochromis* and *Tylochromis*; two predorsals are of more frequent occurrence in Neotropical genera (Cichocki, 1976:182; Oliver, 1984:29).

A single predorsal, usually small and comma-shaped, is visible in radiographs of *N. squamiceps, N. dimidiatus* and some *N. splendens* (the radiographed samples included some paratypes of all three species). It is absent, nevertheless, in all the examined material of the other *Nanochromis* species.

Clearly, there is an apomorphic trend within *Nanochromis* for the predorsal bone to be lost since even when present it is greatly reduced in size, and in at least one species (*N. splendens*) it is more often absent than present.

(3) Cheek and nape scaleless.

Reduced squamation, or its complete suppression in those particular areas of the body, occurs in other cichlids, and is usually associated with torrenticolous habits. But, as was the case with reduced infraorbital bones, the phenomenon in these other taxa is either linked with apomorphic features not shared by *Nanochromis*, or with the plesiomorphic condition of characters which are apomorphic in *Nanochromis*.

As Stewart & Roberts (1984) note, nape and cheek squamation is not greatly reduced in two species, *N. dimidiatus* and *N. squamiceps*, taxa which seem to constitute a plesiomorphic line within the genus. Thus, a scaleless nape and cheek, like the absence of a supraneural bone, could be interpreted as a synapomorphic condition uniting certain species within the genus, but not as one for the genus as a whole.

(4) Five lateralis pores on the mandible and seven on the preopercle, including one at its dorsal tip.

Such numbers for the openings in these canals are apparently universal amongst African cichlids. The character cannot therefore be considered a synapomorphy for *Nanochromis*.

In brief, of the four characters listed by Stewart & Roberts (1984), only the peculiarities exhibited in the infraorbital series can be considered an apomorphy for *Nanochromis* as a whole. It thus joins the extreme dorsal position of the upper lateral line as a defining synapomorphy for the genus.

DIAGNOSIS. *Nanochromis* is distinguished from all other African taxa by the following characters taken in combination: Body attenuated and slender, the dorsal head profile decurved or, if straight, sloping steeply (Fig. 24).

Neurocranial apophysis for the upper pharyngeal bones of the *Haplochromis*-type. Supraoccipital crest low, without a well-defined peak. Fronto-parietal crests weak. Supraethmoid not suturally united with the vomer.

Palatine with a two-point neurocranial contact, anteriorly through an articulation in the region of the ethmovomerine suture, and posteriorly with a facet on the ventral face of the lateral

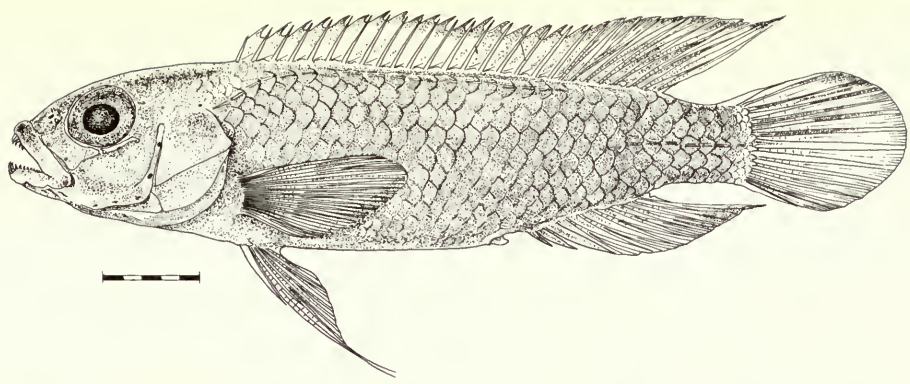

Fig. 24 *Nanochromis nudiceps*; one of the syntypes. Drawn by Gordon Howes. Scale bar in mms. (BMNH 1899.11.27:64).

ethmoid (see Greenwood, 1985*a*): A calyx is formed between the metapterygoid and the hyomandibula.

Infraorbital bone series reduced to the lachrymal and an elongate second bone closely articulated with the lachrymal from which it protrudes in a handle-like manner; there is a prominent pore in the cheek at the posterior end of the second infraorbital, coincident with the last lateralis pore in that bone. Lachrymal with four openings to its laterosensory canal system.

Lower jaw less than 50 percent of the head length. Ascending process of the premaxilla from slightly shorter to slightly longer than the alveolar arm. Anguloarticular with a roofed canal for the mandibulo-preopercular laterosensory canal.

Jaw teeth of the typical group II pelmatochromine type (see p. 158); the first appearance of posteriorly directed teeth situated anterolaterally in the lower jaw is correlated with the size of the fish (see p. 187).

A well-developed, clearly circumscribed, visor-like pad developed in the pharynx immediately anterior to the upper pharyngeal bones. Posterior facing margins of the major upper pharyngeal bones aligned so as to form a broad and shallow V, its apex directed anteriorly. Anterior blade of the lower pharyngeal bone relatively short, its length contained 3–4 times in the overall length of the bone. No 'kukri'-shaped teeth on that bone (see p. 197), the teeth of which all have the tip of the major cusp lying a little anterior to, or in the same vertical as the posterior margin of the tooth.

Scales cycloid, 23–28 in the lateral-line series. Cheek naked or partly scaled; nape and chest seemingly naked in most species (but very small, scattered and deeply embedded scales sometimes present), obviously scaled in others where the nape scales are neither noticeably small nor deeply embedded, but the chest scales are small and confined to the upper part of that region.

Upper lateral-line situated high on the body with, in most species, slightly more than its posterior half contiguous with the dorsal fin base, and with not more than one or one and a half scales between about the fifth pored scale in the series and the first pored scale which is contiguous with the dorsal fin base. Both lateral-line series in all species are often interrupted by the intercalation of several non-pored scales.

Twelve scales around the caudal peduncle.

Gill-rakers of the group II pelmatochromine type, but the tubercles are often small or difficult to detect, and the epibranchial rakers vary from short and broad to relatively slender; 6 to 9 rakers in the outer row of the first ceratobranchial, and 3–5 in a single row on the first epibranchial. Microbranchiospines are absent.

Total number of vertebrae 25–28, comprising 12–14 abdominal and 12–14 caudal elements (excluding the fused PU1 and U1 centra). Predorsal (supraneural) bone absent in five species, present or, more frequently, absent in another, and present but very small and comma-shaped in two others.

Caudal fin apparently showing no sexual dimorphism in the shape of its posterior margin. In all but one species the first pelvic ray in adult males is produced. In females the second ray is as long as or slightly longer than the first ray (a condition also seen in the adult males of *N. transvestitus*). Dorsal fin with 16–19 spines, anal with 3.

Marked sexual dimorphism in the coloration of adults (see p. 187). A dark mark resembling a *Tilapia*-spot occurs in at least two species.

Where breeding habits are known, the species are substrate guarders.

NOTES ON THE ANATOMY AND OTHER FEATURES. The small adult size attained by most *Nanochromis* species, combined with a paucity of material and its often indifferent state of preservation, has severely limited the amount of anatomical information which could be gained. Certain osteological data were obtained from radiographs of all described species, and certain soft anatomical features and osteological characters were studied from partial dissections of *N. nudiceps*, the type species, and *N. parilius* (one specimen of each).

The *neurocranium* of *N. nudiceps* (Fig. 25) has a very low supraoccipital crest whose dorsal margin slopes gently upwards at a low angle; the anterior point of the supraoccipital lies in a vertical passing through the middle of the orbit. Judging from radiographs, the situation is similar

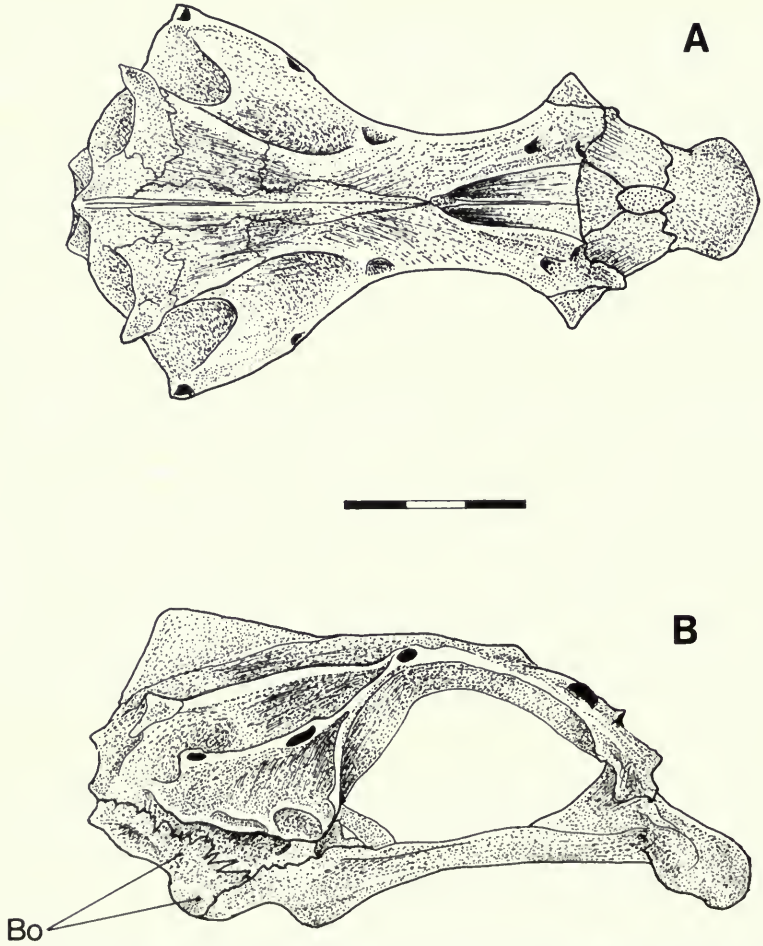

Fig. 25 Neurocranium of *Nanochromis nudiceps* in: A. Dorsal, and B. Right lateral view. Scale bar in mms. (Unregistered specimen; see text, p. 141). Bo = basioccipital.

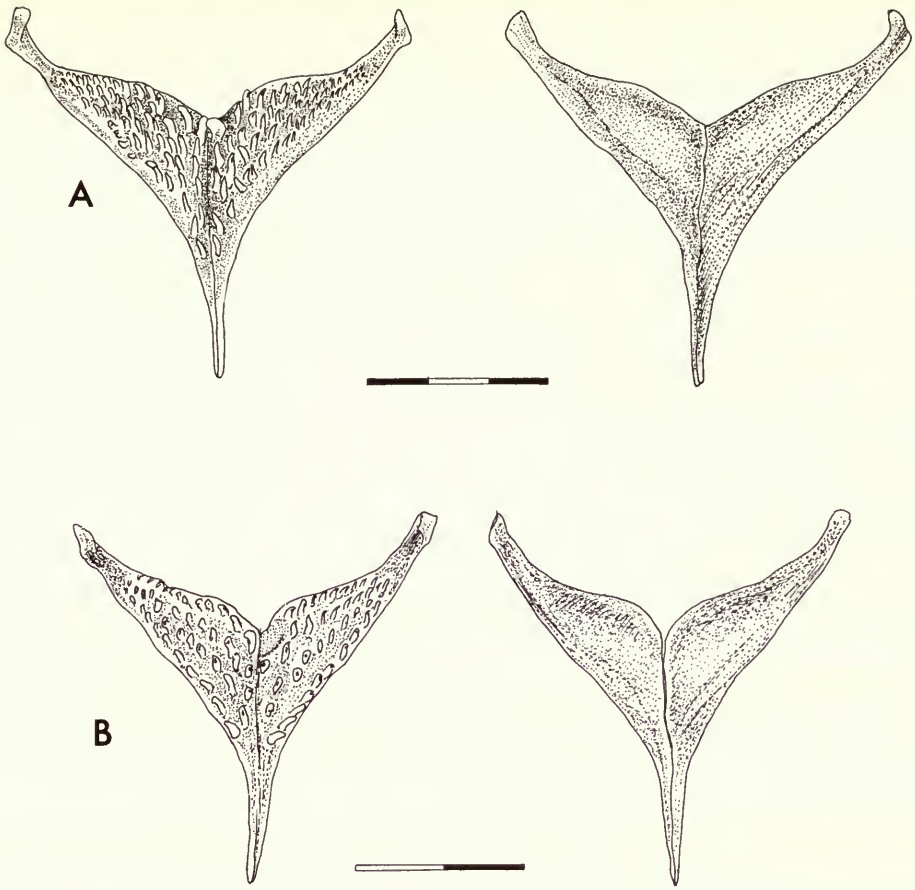

Fig. 26 Lower pharyngeal bones (dentigerous surface left, and ventral surface right) of: A. *Limbochromis robertsi*; holotype. B. *Nanochromis nudiceps* (unregistered specimen, see text, p. 141).

in all other species. The fronto-parietal crests are low and narrow. The ethmovomerine region, whose length is contained about $3\frac{1}{2}$ times in the neurocranial length, slopes at an angle of *ca.* 30° to the horizontal, its tip lying well below the level of the parasphenoid and the apophysis for the upper pharyngeal bone. That apophysis is of the *Haplochromis*-type, with substantial contributions by the basioccipital to its articular surface. The lateral commissure is broad and of the *Haplochromis*-type; no precommissural bridge is present (see Greenwood, 1986).

Apart from the low supraoccipital crest, the weaker fronto-parietal crests, and a narrower interorbital region, the neurocranium of *N. nudiceps* more closely resembles that in most *Pelvicachromis* species than it does the neurocranium in *Parananochromis longirostris* (see pp. 172 & 177 respectively).

What little information that could be obtained on other aspects of the cranial osteology (*jaws* and *suspensorium*) and of the *branchial skeleton*, suggests that no features depart significantly from those of other pelmatochromine taxa. However, it must be remembered that only one partial dissection was possible.

In all *Nanochromis* species the *lower pharyngeal bone* has a deep indentation in its posterior margin, and a short anterior blade which is contained *ca.* 3–4 times in the overall length of the bone, features which impart an arrowhead-like outline to the bone (Fig. 26B). Teeth on this bone are fine (except for the slightly larger teeth in the posterior transverse row, and those posteriorly in the median rows), are weakly cuspidate, and are fairly widely spaced.

The shape and orientation of the *upper pharyngeal bones* in all species are of the common cichlid type, with the near-ovoid upper pharyngeal bones of each side forming a deep and shallow V, its apex directed anteriorly. No other details are available for the pharyngobranchial skeleton.

The peculiar and particular arrangement of the two *infraorbital bones* present (the lachrymal and an elongate second bone) has been touched upon above (p. 181). In all species except *N. dimidiatus* and *N. squamiceps* the upper margin of the elongate second bone is virtually straight, and so does not conform closely to the posteroventral margin of the eye-ball. In outline, the lachrymal and the second bone resemble a simple drawing of a saucepan (Fig. 27).

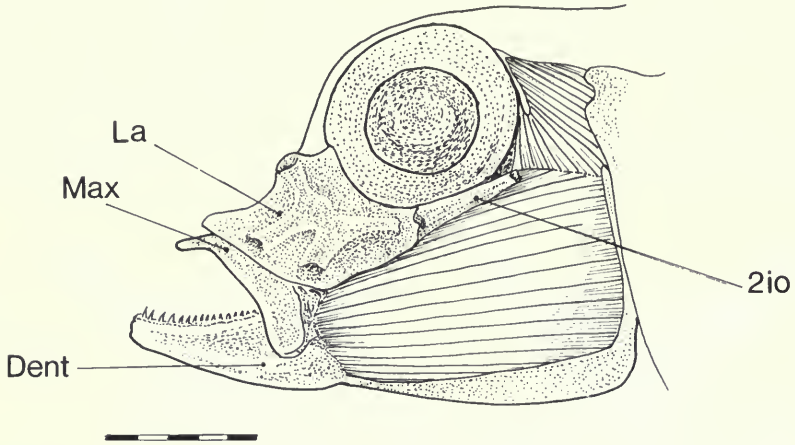

Fig. 27 The two infraorbital bones of *Nanochromis nudiceps* shown *in situ*. Scale bar in mms. (Same specimen as in Fig. 25). La = lachrymal; 2io = second infraorbital bone; Max = maxilla; d = dentary.

The two exceptional species have a second infraorbital whose upper margin is distinctly curved and so follows closely the eye's lower contours; the 'saucepan' outline is thus less obvious.

It has proved impossible to determine whether, ontogenetically, the second infraorbital is a single or a compound element. Some intraspecific variability exists in the number of laterosensory canal pores in this bone, with three being the usual condition but with only two pores sometimes present, either uni- or bilaterally. Four openings are invariable in the lachrymal.

The *squamation* in *Nanochromis* shows several unusual features. The high position of the upper lateral-line in all species, and the contiguity of somewhat more than its posterior half with the base of the dorsal fin in all but two of those, is one of the diagnostic apomorphies for the genus (see p. 183). Even in *N. squamiceps* and *N. dimidiatus*, the species with only the last 3–5 pored scales touching the dorsal fin base, more than the posterior two-thirds of the line is separated from the fin base by only a single scale.

Nanochromis squamiceps and *N. dimidiatus* also differ from their congeners in having the nape fully scaled (naked or with a few, small, scattered, and deeply embedded scales in the other species), and in the chest being partly scaled, but with the ventral and ventrolateral aspects naked. The chest is completely naked in all other *Nanochromis*.

In these species too, and unlike *N. squamiceps* and *N. dimidiatus*, the ventral face of the belly is naked from the pelvic fin insertions to the vent. The cheek in *N. squamiceps* is partially covered by three rows of scales, but there is an extensive naked area anteroventrally; this extends from the posteroventral margin of the lachrymal downwards to the preoperculum, and posteriorly almost to below the mid-point of the orbit. In the *N. dimidiatus* type specimens examined, the naked area is even larger, with only one or two scales present below the second infraorbital bone; these specimens, however, are now in a very poor condition so some scales could have been lost. The cheek is entirely naked in all other *Nanochromis* species.

Gill-rakers in *Nanochromis* are basically of the group II pelmatochromine type discussed on p. 159. There are 6–9 rakers in the outer row of the first ceratobranchial. Departure from the modal group II type of raker is manifest in the very small tubercles developed on the concave upper surface of the first ceratobranchial rakers; these may appear smooth when examined at a low magnification despite the large number of tubercles present.

Some, and apparently interspecific, variation occurs in the degree to which the median membrane between the inner and outer rows of rakers is developed on the first arch. But, as noted before, this could be a reflection of the specimens' state of preservation.

Only a single row of 3–5 epibranchial rakers is present on the first arch, and these vary interspecifically, from short and broad to slender and elongate.

As in other group II pelmatochromines, there are no microbranchiospines.

The *dentition* of *Nanochromis* shows no marked departure in tooth form or pattern from that of other group II pelmatochromines (see p. 158).

Because the size range of available specimens is so limited it has not proved possible to determine at what standard length the posteriorly orientated anterolateral dentary teeth first appear, or whether the definitive tooth form is preceded by one of a different kind (see pp. 144 & 158). In the sample of *N. transvestitus* examined, the smallest individual with posteriorly directed teeth in the dentary has a standard length of 24 mm, and the smallest *N. parilius* with such teeth is 31 mm SL.

The *vertebral column* is composed of 12–14 abdominal, and the same number of caudal elements (excluding the fused PU1 and U1 centra), giving total counts of 25–28.

In the single syntypical specimen of *N. squamiceps*, and the four syntypes of *N. dimidiatus* radiographed, a small, comma-shaped *predorsal bone* is present, as it is in two of the 10 *N. splendens* paratypes examined. In the specimens of all other species no trace of a predorsal bone is visible in the radiographs.

There apparently is no sexual dimorphism in the shape of the *caudal fin* margin, which is rounded in both sexes. The first branched *pelvic ray* of adult males is clearly the longest, although in some individuals the second ray can be almost as long as the first. Females have the second branched pelvic ray as long as, or slightly longer than the first, as is apparently the case in both sexes of *N. transvestitus*. (For a discussion of this character, see p. 169).

There are 16–19 spinous rays in the *dorsal fin* and 3 in the *anal*.

The little information gained from a partial dissection of a *N. nudiceps* specimen showed no outstanding features in the *myology and arthrology* of the jaws. No data are available for the *pharyngeal* and *branchial musculature*.

Coloration. All species of *Nanochromis* have a marked sexual dimorphism in adult coloration (see Roberts & Stewart, 1976, and especially the colour photographs in Linke & Staeck, 1981); one species, *N. transvestitus* is very unusual amongst African cichlids in having the female more brightly coloured than the male (Stewart & Roberts, 1984).

At least two species, *N. splendens* and *N. dimidiatus*, seem to have a *Tilapia*-spot on the soft dorsal fin of some individuals (Roberts & Stewart, 1976:29; and Linke & Staeck, 1981: 63, for the species respectively). *Nanochromis dimidiatus* females, when adult, are also interesting in that a silver blotch is developed on the flank above the genital opening. A similar silver mark is otherwise known only in *Thysia* (see Loiselle & Welcomme, 1972; colour photograph in Linke & Staeck, 1981:135), and in specimens identified by Voss (1980:23, 25 & 27) as *Pelvicachromis subocellatus*. Such a mark has not been recorded, as far as I am aware, in other African cichlids.

Breeding biology. All species of *Nanochromis* are substrate guarders; for detailed accounts of spawning habits see Linke & Staeck (1981).

Included species: Nanochromis nudiceps (Blgr) 1899; *N. consortius* Roberts & Stewart, 1976; *N. dimidiatus* (Pell.) 1904; *N. minor* Roberts & Stewart, 1976; *N. parilius* Roberts & Stewart, 1976; *N. splendens* Roberts & Stewart, 1976; *N. squamiceps* (Blgr) 1902; *N. transvestitus* Stewart & Roberts, 1984.

Intrageneric relationships

If it be accepted that the interrupted and reduced series of infraorbital bones (see p. 181 above), and the high-set upper lateral-line with at least the last 3–5 pored scales contacting the dorsal fin base,

are unifying synapomorphies for *Nanochromis*, then two groups of species can be recognised within the genus.

The smaller group, comprising the species *N. squamiceps* and *N. dimidiatus* is characterised by having only the last 3–5 pored scales of the upper lateral-line contiguous with the dorsal fin base, a completely scaled belly and nape, a partially scaled chest and cheek, and by the presence of a predorsal bone (albeit reduced and comma-shaped) in all individuals.

The second and larger group, contains all the remaining species. It is characterised by having the posterior half (or slightly more) of the upper lateral-line contiguous with the dorsal fin base, a naked nape, cheek and belly, and by the absence of a predorsal bone (at least in the majority of individuals, see p. 187 above). In all these features members of the group exhibit a more derived state than is shown by either *N. squamiceps* or *N. dimidiatus*.

For the moment it would seem preferable to treat the two groups informally and not recognise them as subgenera. That decision, however, may well be revised when more is known about the soft anatomy, the osteology and the breeding habits of all *Nanochromis* species.

LIMBOCHROMIS gen. nov.

TYPE SPECIES: *Nanochromis robertsi* Thys van den Audenaerde & Loiselle, 1971.

SYNONYMY. *Nanochromis* (*non* Pellegrin, 1904): Thys & Loiselle, 1971 (the species *robertsi* and *cavalliensis*).

ETYMOLOGY. From the Latin *limbus*, an edge, and *chromis*; *limbus* in this particular context is used more in the spirit of its common English form of 'in limbo'.

This new genus represents a taxonomic defeat. It is established for two species which, although clearly members of the group II pelmatochromine assemblage, cannot be included in any of the genera recognised here, nor can it be identified as a sister group to any of those taxa.

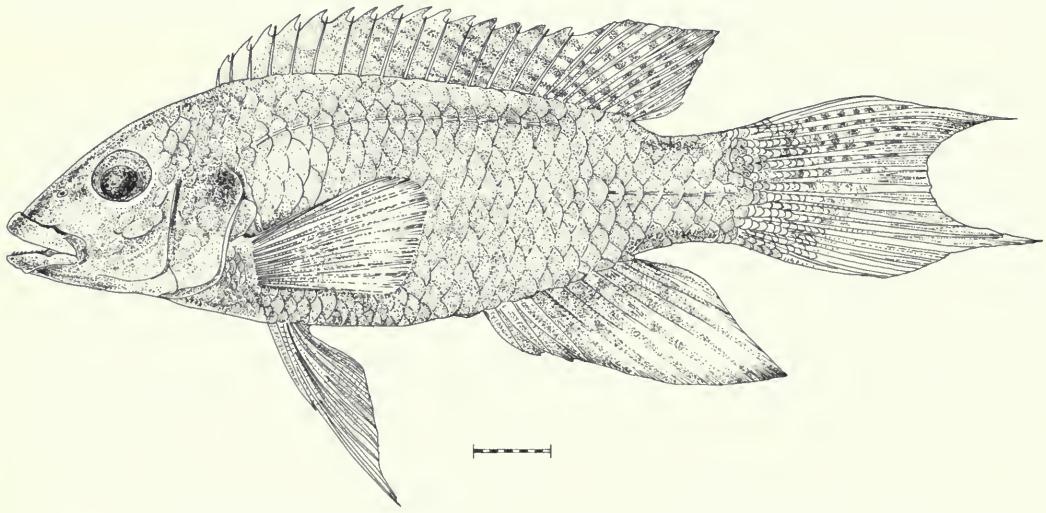

Fig. 28 *Limbochromis robertsi*; holotype (SU 63143). Scale bar in mms. Drawn by Gordon Howes.

Thys & Loiselle (1971:20), with obvious misgivings, referred their two new species to *Nanochromis* (*sensu* Thys, 1968*a*) simply because both have a reduced number of circumpeduncular scales, namely 12–14. The authors noted that both species differed from the concept of *Nanochromis* which they were using in having the caudal fin margin produced into a pair of streamer-like points, and that the geographical distribution of both species lay outside the range of other species referred to that genus (then treated as a subgenus) by Thys (1968*a*).

As *Nanochromis* is now restricted to species having part of the lateral-line contiguous with the dorsal fin base, only two infraorbital bones, and a *Haplochromis*-type of neurocranial apophysis for the upper pharyngeal bones (see pp. 182–184), neither *robertsi* nor *cavalliensis* can be considered members of that genus. In both species the upper lateral-line is completely separated from the dorsal fin base (by at least one scale at its nearest point of approach to the fin), the infraorbital series is complete, and the neurocranial apophysis is of the plesiomorphic *Tilapia*-type. Furthermore, neither species has, in either sex, the length of the second branched pelvic ray equal to, or slightly longer than the first ray.

The pelvic fins and the plesiomorphic condition of the neurocranial apophysis in *robertsi* and *cavalliensis* serve to exclude the species from membership of the genus *Parananochromis*, a taxon which, in their general habitus, they resemble more than they do any species of *Nanochromis*.

Again, the nature of the pelvic fins excludes *robertsi* and *cavaliensis* from *Pelvicachromis* (see p. 169), as does the reduced number of circumpeduncular scales (12 or 13 in *cavalliensis*, 14 in *robertsi*, compared with 16 in all *Pelvicachromis* species). The plesiomorphic pharyngeal apophysis in both *Pelvicachromis* and the two species under review, is, of course, valueless for establishing any possible relationship between them.

It is for these various reasons that I have erected the genus *Limbochromis* for the species *robertsi* and *cavalliensis*. Its monophyly would seem to be attested by a reduced number of scales around the caudal peduncle occurring in species which do not share, with other pelmatochromines having that feature, the derived *Haplochromis*-type pharyngeal apophysis on the skull or an elongate second pelvic fin ray in females.

The question then arises as to whether or not the reduced peduncular scale count in *Limbochromis* indicates its relationship, as the plesiomorphic sister group, to *Parananochromis* and *Nanochromis* combined. Here one is faced with a dilemma which I do not think can be settled until more information is available about the four taxa which must be involved in solving that problem, viz. *Limbochromis, Pelvicachromis, Parananochromis* and *Nanochromis*.

The three latter taxa share one apparently synapomorphic feature, namely, pelvic fins in females which have the second branched ray longer than the first. *Parananochromis* and *Nanochromis*, however, have the derived *Haplochromis*-type pharyngeal apophysis but *Pelvicachromis* has the plesiomorph *Tilapia*-type; the two former species have a reduced (i.e. derived) number of scales around the caudal peduncle but *Pelvicachromis* does not.

Thus, using their one synapomorphic feature (pelvic fins), *Pelvicachromis* could be interpreted as the plesiomorphic sister taxon of *Parananochromis* and *Nanochromis*. If that argument is accepted, then the reduced circumpeduncular scale count, the only derived character shared by *Limbochromis* and the *Nanochromis-Parananochromis* generic pair, is not a synapomorphy but a homoplastic feature.

As a counter argument one could propose that the reduced scale count is the true synapomorphy (shared by *Limbochromis* and the *Nanochromis-Parananochromis* pair) and that the pelvic fin feature is the homoplastic one independently derived in *Pelvicachromis*. In this case, *Limbochromis*, would be the plesiomorphic sister taxon of the *Nanochromis-Parananochromis* generic pair.

In the absence of other and differentially congruent synapomorphic features which might refute one or other of those arguments, either solution would seem equally parsimonious (see also p. 194).

DIAGNOSIS. Since so little material of either species is available for study, the diagnosis is, perforce, based essentially on superficial characters. *Limbochromis* (Fig. 28) closely resembles *Parananochromis* except that:

(1) The neurocranial apophysis for the upper pharyngeal bones is of the *Tilapia*-type, *i.e.* formed entirely from the parasphenoid.

(2) There are 12–14 (modally 12 or 13) scales around the caudal peduncle.

(3) The first branched pelvic fin ray in adult females is clearly longer than the second ray; dorsal fin with 15 or 16 spines.

(4) Bilateral naked patches are present on the chest in one species.

(5) The upper lateral-line at its highest point (the 8th pored scale) is separated from the dorsal fin

base by two large and one very small scale, or by $1\frac{1}{2}$ scales; posteriorly, the last 3 or 4 pored scales are separated from the fin base by $1\frac{1}{2}$ scales, or by one large and one very small scale; lateral-line with 28 or 29 scales; chest scales moderately small, with a fairly abrupt size transition between them and those on the ventrolateral aspects of the flanks and belly.

(6) Vertebral column with 26 vertebrae (excluding the fused PU1 and U1 centra) comprising 13 or 14 abdominal and 12 or 13 caudal elements.

(7) Caudal fin in adult males of one species (*L. robertsi*) with two, symmetrically produced streamers; probably with two shorter projections in females. Nature of caudal fin margin in adult males unknown for the second species (*L. cavalliensis*), but adult females have a short projection; caudal margin subtruncate to rounded in young.

(8) No data available on live colours in *L. cavalliensis*, but there is pronounced sexual dimorphism in *L. robertsi* (see Linke & Staeck, 1981: 74–75).

NOTES ON THE ANATOMY AND CERTAIN OTHER FEATURES. Because no deep dissections could be made on the few available specimens, and since no osteological preparations exist, virtually nothing can be said about the musculature and the skeleton of *Limbochromis*. Those characters which could be investigated by superficial dissection, and from radiographs, do not depart greatly from the usual pelmatochromine group II condition or, indeed, from that of the pelmatochromines as a whole.

The *dentition and gill-rakers* are typically those of group II pelmatochromines, as is the absence of microbranchiospines (see p. 157). Nothing is known about size-correlated changes in tooth form, or at what size the posteriorly directed anterolateral teeth in the dentary first appear.

The shape of the *lower pharyngeal bone* (Fig. 26A) and the nature of the *lower pharyngeal teeth* show no outstanding features, and the shape, dentition and orientation (a broad, shallow V) of the *upper pharyngeal bones* are like those in other group II pelmatochromine species.

One unusual feature, with respect to most other pelmatochromines, is the occurrence, in one species, of five rather than four openings to the *lachrymal laterosensory canal* system. The occasional occurrence of five openings in *Pelvicachromis* has been reported (but not confirmed) by Trewavas (1983) and five openings are usual in all but one species of *Chromidotilapia* (see p. 168).

It is obvious that some sort of sexual dimorphism occurs in the shape of the *caudal fin* margin (see Thys & Loiselle, 1971), but its exact nature is still undetermined. The seemingly symmetrical development of streamer-like prolongations from both the upper and lower lobes of the caudal fin's posterior margin in one species (*L. robertsi*; see Fig. 28) is unusual amongst African cichlids, but seems to be repeated, albeit weakly, in the other species of *Limbochromis*. More information is needed about this feature, as are detailed accounts of live colours in sexually active fishes.

Judging from the radiographs, *neurocranial shape* in *Limbochromis* is like that in *Paranano-chromis*. A well-developed, dagger-like *predorsal (supraneural) bone* is present. The *vertebral column* has 13 or 14 (mode) abdominal, and 12 (mode) or 13 caudal centra (excluding the fused PU1 and U1 centra), with a total count of 26.

As in some other group II pelmatochromines, the upper *lateral-line* in *Limbochromis* has a relatively high position on the body, with its highest point (the 8th pored scale) separated from the dorsal fin base by $1\frac{1}{2}$ to 2 large and one very small scale; posteriorly, the last 3 or 4 pored scales are separated from the fin base by $1\frac{1}{2}$ scales or one large and one very small scale. The cheek is partly covered by 3 or 4 rows of scales, with a large naked area anteroventrally, and in one species, a narrow, naked strip below the scaled area. Chest scales are small, and have a relatively abrupt size transition with those on the ventrolateral aspects of the flanks. In *L. robertsi*, but not in *L. cavalliensis*, the scales on the medioventral aspect of the chest are somewhat larger than those occurring laterally (i.e. as in *Parananochromis*, see p. 179); *L. cavalliensis*, but not *L. robertsi*, has a small and bilateral naked patch on the anterolateral aspect of the chest.

What information there is on the *breeding biology* of the two *Limbochromis* species (see Thys & Loiselle, 1971: 198, 199, and 202–203), does not indicate that either is a mouth-brooder.

Included species. Limbochromis robertsi (Thys & Loiselle) 1971, and *Limbochromis cavalliensis* (Thys & Loiselle) 1971.

The phylogenetic relationships of the pelmatochromine taxa

One of the objects of this paper is to investigate whether the pelmatochromine fishes of Thys (1968*a*, see p. 139) are a distinct and monophyletic lineage within the African Cichlidae, and if that is so, what is their relationship to other African lineages.

For the moment, Thys' (1968*b*) transfer of his subgenus *Pelmatochromis (Pelmatochromis)* to *Tilapia* will be ignored; his action was challenged and rejected by Trewavas (1973), and my reasons for rejecting it will be discussed later (p. 195). Thus the pelmatochromine genera concerned are those originally defined by Thys (1968*a*) as subgenera of *Pelmatochromis*, and subsequently modified by Loiselle & Welcomme (1972), Trewavas (1973 & 1974) and in this paper.

The genera involved are: *Pelmatochromis* Steindachner, *Thysia* Loiselle & Welcomme, *Chromidotilapia* Blgr, *Pelvicachromis* Thys, *Parananochromis* gen. nov., *Nanochromis* Pellegrin, and *Limbochromis* gen. nov.

For the purposes of this discussion, a monophyletic lineage is recognised by all its constituent taxa uniquely sharing one or more derived characters which would suggest their having stemmed from a recent common ancestor with that or those features. Thus, although all pelmatochromines have at least two supposedly derived features, cycloid scales and unicuspid oral teeth when adult (see p. 143), these are shared with a large number of other taxa: I would interpret that level of synapomorphy as possibly indicative of a remote rather than a recent shared ancestry, if it is not an example of homoplasy.

As indicators of recent common ancestry I have chosen those synapomorphic features which are shared by fewer species, using the extent of their occurrence amongst different taxa to build up various hierarchical levels of relationship. For example, a well-developed, visor-like hanging pad developed from the pharyngeal roof (p. 157) is a derived feature shared by several pelmatochromines, and is congruent with four other apomorphic features (see pp. 157–160). In brief, they involve the absence of microbranchiospines, the morphology of the oral teeth, and the morphology of the gill-rakers on the first gill-arch. The apomorphic status of all these characters is based on outgroup comparisons within the family, the suborder Labroidei and other percoid fishes as well.

A sixth character may also indicate a common ancestry for this group, but it occurs mosaically and its derived status has still to be ascertained with certainty. This feature is the presence of a well-defined silver spot or blotch situated immediately above the ano-genital region of sexually active female fishes. It has been recorded in *Thysia*, one *Pelvicachromis* species, and in *Nanochromis dimidiatus* (see respective generic descriptions for references). Unfortunately, live colours are known for relatively few cichlids, thus making it impossible to determine, with reasonable certainty, whether this seemingly derived characteristic is indeed an apomorphy.

The five principal synapomorphies noted above occur together in *Thysia, Chromidotilapia, Pelvicachromis, Parananochromis, Nanochromis* and *Limbochromis*, and are taken to indicate the monophyletic status of that assemblage, the individual genera of which are themselves defined on the basis of each having one or more of its own autapomorphic characters.

The two remaining pelmatochromines, *Pelmatochromis* and the monotypic *Pterochromis*, share none of the five features discussed above; the relationship of *Pterochromis* can be dealt with rapidly, but regrettably, rather unsatisfactorily.

Pterochromis shares no derived features with either *Pelmatochromis* or, as noted above, with the *Thysia-Limbochromis* complex, except of course for those suggesting relationship at a much more inclusive level than we are concerned with here.

The unicuspid teeth of *Pterochromis*, relatively stout and with conical crowns, are of a generalized type amongst unicuspids, and are quite unlike those in the *Thysia-Limbochromis* group. Its long, slender and fine gill-rakers on the first arch are a derived feature, but are unique amongst the taxa under discussion (including *Pelmatochromis*). Similar rakers do occur within the tilapiine cichlids (*sensu* Trewavas, 1983) but *Pterochromis* does not share a single derived feature with any tilapiine taxon. The gill-rakers, therefore can be considered an autapomorphic feature for *Pterochromis*.

Likewise, the elongate lower jaw, long premaxillary ascending processes, and the steeply inclined

mouth of *Pterochromis* must be considered autapomorphies since none is congruent with other derived features occurring in taxa sharing those particular oral specialisations.

Thys (1968*a*) and Trewavas (1973) suggest that *Pterochromis* is a specialised form derived from *Pelmatochromis ocellifer*, but neither author discussed that idea in any detail; the proposed relationship would seem to be based on the shared plesiomorphic characters of the two taxa. Certainly no unique synapomorphies are shared by them, thus making it impossible to establish such a phylogenetic history.

The inadequate study material of *Pterochromis* has severely restricted investigations of its anatomy and osteology, and almost nothing is known about the biology of the species. Thus, for the moment, and based only on the superficial features discussed here and on page 155, I can suggest no testable hypothesis of relationship for the genus, and would exclude it from even an informal association with the other pelmatochromine taxa.

Pelmatochromis provides a rather different sort of problem. Like *Pterochromis* it shows few derived features, has well-developed microbranchiospines, and lacks a visor-like pharyngeal hanging pad, thus excluding it from actual membership of the *Thysia-Limbochromis* group (see p. 157).

Indeed, there seems to be not a single unequivocal autapomorphy on which to define the genus (see p. 146). Its status as a discrete taxonomic entity is therefore based simply on its having a suite of characters, both apo- and plesiomorphic which, taken in combination, distinguish it from other and superficially similar taxa.

Pelmatochromis, like *Pterochromis,* has unicuspid outer row jaw teeth, and as in the latter genus, their cusp form is of a simple conical type, differing from the compressed-conical cusps in members of the *Thysia-Limbochromis* group (see p. 157); also, unlike members of that group, *Pelmatochromis* has no posteriorly directed teeth situated anterolaterally in the lower jaw.

The outer row gill-rakers on the first ceratobranchial of *Pelmatochromis* species are very unlike those in *Pterochromis* and, indeed, those in the majority of African cichlids. Their closest morphological counterparts are to be found in members of the *Thysia-Limbochromis* lineage. They could, in fact, be described as somewhat simplified versions of the rakers in that lineage (see p. 146).

Gill-rakers, then, are the sole derived features in *Pelmatochromis* which might indicate its relationship. With only that character available I would, at best, suggest an informal and very tentative status for *Pelmatochromis* as the putative and plesiomorphic sister group of the *Thysia-Limbochromis* lineage. Certainly, and unlike *Pterochromis*, there are no apomorphic features

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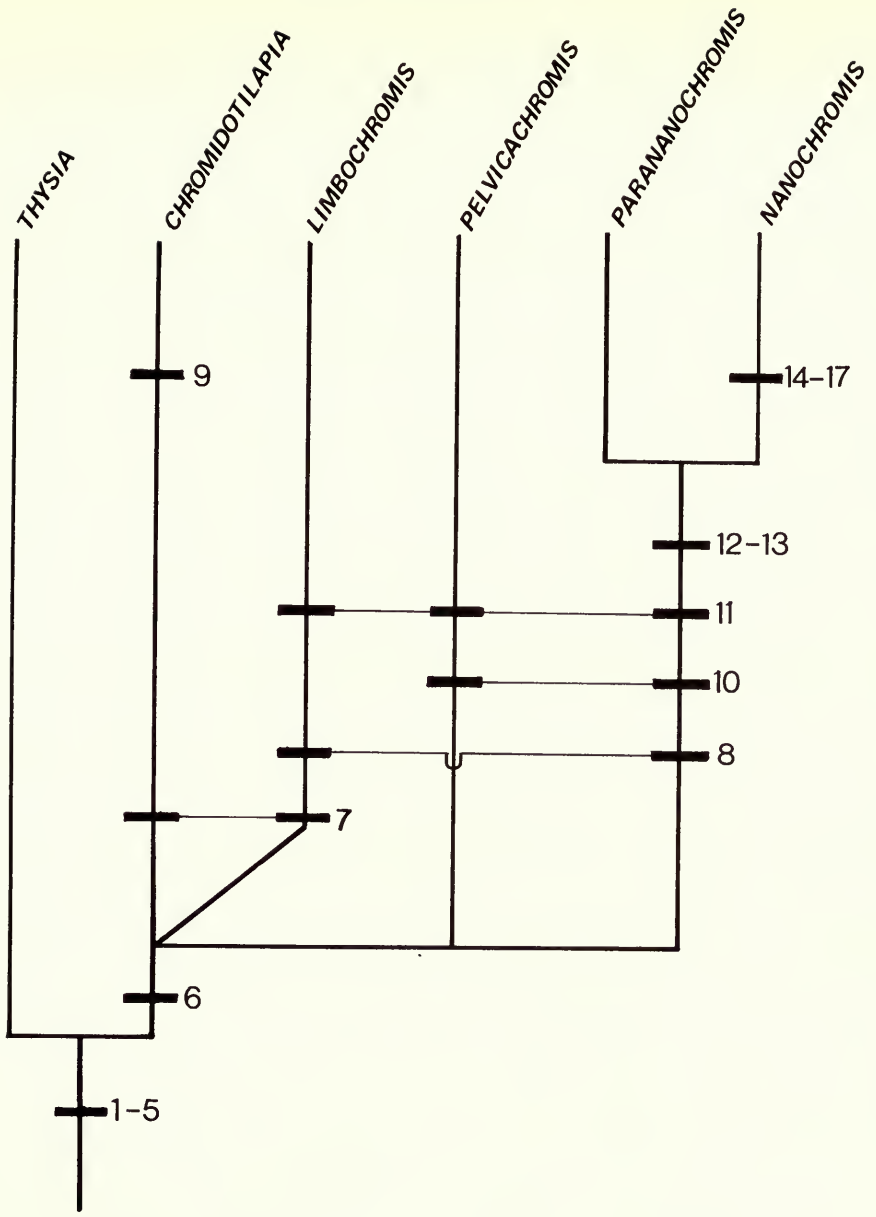
Fig. 29 Diagram showing the distribution of various derived features amongst the chromidotilapiine cichlids (see pages 194–195); this figure can be used as a key to the genera. (1) Visor-like hanging pad in the pharynx (p. 157). (2) Outer teeth in both jaws unicuspid, with the labial surface of the crown flattened and the lingual aspect convex, resulting in the crown having well-defined and acute margins (p. 158 & Fig. 8). (3) A few teeth situated anterolaterally in the lower jaw so orientated that the crowns point posteriorly and not buccally (Fig. 9). (4) No microbranchiospines. (5) Ceratobranchial gill-rakers in the outer row of the first gill-arch pachydermatous, transversely aligned, with a tuberculate and concave upper surface and a protracted distal tip (p. 159 & Fig. 11). (6) Two large scales and one very small scale, or fewer scales ($1\frac{1}{2}$ the modal number) between the dorsal fin base and the highest point of the upper lateral line (the 8th or 9th pored scale). (7) Five openings to the laterosensory canal system in the lachrymal (1st infraorbital) bone (but one species in each genus with only four openings). (8) 12–14 scales around the caudal peduncle. (9) Mouth brooders. (10) The 2nd (sometimes the 2nd and 3rd) branched pelvic fin ray of females longer than the 1st branched ray, giving the distal tip of the fin a rounded rather than a pointed appearance. (11) Small to very small scales on the chest (which is entirely naked in some species, and has naked areas in a few others). (12) Neurocranial apophysis for the upper pharyngeal bones formed by the parasphenoid and basioccipital bones (i.e. of the *Haplochromis*-type), see p. 178. (13) Twelve scales around the caudal peduncle. (14) Only two bones in the infraorbital series (the lachrymal and one other bone articulating with it; see p. 186). (15) At least the last 3 or 4 pored scales of the upper lateral line contiguous with the fin base in most species. (16) Predorsal (supraneural) bone absent in many species, small and reduced in the others; see p. 187. (17) Supraoccipital crest low.



shown by *Pelmatochromis* which would preclude its representing a morphotype from which the less derived members of the *Thysia-Limbochromis* line could have evolved.

In brief, out of the original, if somewhat informally recognised pelmatochromine group of Thys (1968*a*), one monophyletic assemblage can be recognised on the basis of various synapomorphies. It comprises the genera *Thysia, Chromidotilapia, Pelvicachromis, Limbochromis, Parananochromis* and *Nanochromis*. As an informal epithet for that lineage, I propose the term 'chromidotilapiines'.

The two remaining genera, *Pterochromis* and *Pelmatochromis* are currently of indeterminable phyletic affinity, although there is some suggestion that *Pelmatochromis* might be the sister group of the chromidotilapiines (see above).

The intrarelationships of the chromidotilapiines

A tentative intragroup phylogeny for the chromidotilapiines is set out in Fig. 29.

The first dichotomy is based on the number of scales between the highest pored scale in the upper lateral-line (usually the 8th or 9th) and the base of the dorsal fin. *Thysia*, having the highest count ($2\frac{1}{2}$ or 3 scales) and sharing no other derived features with the other species, except the group synapomorphies discussed earlier, is taken to be the plesiomorphic sister taxon to all the others combined.

The derived characteristic of these other taxa lies in their having the dorsal fin base separated from the high-point of the lateral-line by no more than two large and one very small scale, or, as is modal for the group, one and a half or one scale.

The first division of this group is in the form of an unresolved polychotomy caused by *Limbochromis* (see discussion on p. 189). That genus shares some derived features with the more apomorphic members, but its apomorphies are combined with certain plesiomorphic features which are represented apomorphically in the other taxa. *Pelvicachromis* occupies, as it were a 'mirror-image' position with respect to the same characters.

In addition to the possible relationships discussed on p. 189, a fully resolved cladogram could be produced if two other assumptions were made. First, that the apparent plesiomorphy of the high circumpeduncular scale count in *Pelvicachromis* actually represented a secondary, that is derived, return to the plesiomorphic condition from the low counts in *Limbochromis, Parananochromis* and *Nanochromis*. Second, that the derived number of laterosensory pores (5 cf. 4) in certain *Chromidotilapia* and *Limbochromis* species represents a homoplastic rather than a synapomorphic feature. Such a cladogram, based on those assumptions and employing the other characters used in Figure 29, would make *Limbochromis* the plesiomorphic sister group of *Pelvicachromis, Parananochromis* and *Nanochromis* combined, and *Pelvicachromis* the plesiomorphic sister taxon of *Parananochromis* and *Nanochromis*.

However, since the two assumptions are untestable at present, this solution is no more satisfactory than that discussed before (p. 189). Thus, for the moment, a polychotomous arrangement would seem to be the only acceptable one.

Within the polychotomy, *Chromidotilapia* and *Limbochromis* have retained the plesiomorphic condition of the pelvic fin in females, with the first branched ray longer than the second, as it is in males also. *Chromidotilapia* has slightly more scales (2 plus one very small scale) above the high-point of the lateral-line and the dorsal fin base than does one species of *Limbochromis* (the other has the same number as *Chromidotilapia*). *Chromidotilapia* also retains the plesiomorphic feature of large chest scales (small, sometimes with naked areas in the other taxa). No data are available on the breeding habits of *Limbochromis*, but *Chromidotilapia*, uniquely amongst the chromidotilapiines, is a mouth brooder. Another derived feature in that genus is the presence of five laterosensory canal openings in the lachrymal (but one species retains the plesiomorphic number of four); however, one of the two *Limbochromis* species also has five openings. Both *Limbochromis* species show the derived condition of a reduced scale count around the caudal peduncle, a feature not shared with either *Pelvicachromis* or *Chromidotilapia*, but one shared with two members of the fourth branch to the polychotomy, namely *Nanochromis* and *Parananochromis*. Both *Chromidotilapia* and *Limbochromis*, like *Pelvicachromis*, have the plesiomorphic *Tilapia*-type pharyngeal apophysis on the skull base.

Pelvicachromis together with the *Parananochromis–Nanochromis* generic pair, are characterised by having the derived pelvic fin condition where, in females, the second or second and third branched rays are longer than the first ray. Other synapomorphies shared by the three taxa (and approached by *Limbochromis*) are their small to very small chest scales abruptly size-demarcated from the scales on the ventrolateral aspects of the flanks, and a further reduction in the number of scales ($1\frac{1}{2}$, rarely 2) between the high-point of the upper lateral-line and the dorsal fin base; again a characteristic found in one *Limbochromis* species.

A major dichotomy in this assemblage is that between *Pelvicachromis* with its plesiomorphic *Tilapia*-type pharyngeal apophysis, and *Parananochromis* and *Nanochromis* which have the

derived *Haplochromis*-type. Both the latter genera are further linked by sharing a reduced number of scales around the caudal peduncle, 12 as compared with 16 in *Pelvicachromis*.

The dichotomy between *Parananochromis* and *Nanochromis* is based on three autapomorphic features of the latter taxon, viz. only two bones in the infraorbital series (see p. 186), at least the posterior quarter and usually the posterior half of the upper lateral-line contiguous with the dorsal fin base, and the predorsal bone either absent or, in a few species, very greatly reduced in size. Furthermore, in all but two *Nanochromis* species the scales on the chest are also greatly reduced in size, often with large naked areas, and in some species are completely absent (see p. 186).

In most respects this hypothesis of relationships within the chromidotilapiines is both inadequate and unsatisfactory. It can only be considered as a target for further attempts based on more detailed anatomical studies and the use of other and non-morphological characteristics.

From an evolutionary point of view the various chromidotilapiine genera, from *Thysia* at one extreme to *Nanochromis* at the other, show a clear cut reductional trend in a number of characters. These involve the overall body shape (from deep and barely compressed to slender and elongate), a decrease in the number of scales between the lateral-line and the dorsal fin base, a reduction in the number of scales around the caudal peduncle, and a reduction in the size of the scales on the chest (leading to partial or complete suppression in some taxa).

The contrast between the end-points of these trends, as represented by *Thysia* and *Nanochromis*, is very marked, yet within the assemblage the trend is certainly a very gradual one with the various stages represented by species of different genera. That phenomenon provides an interesting parallel with a similar pattern of change, but one involving different characters, amongst the endemic haplochromine species of Lake Victoria, and for which the term cladistic gradualism was coined (Greenwood, 1981; 1984*b*).

Intrafamilial relationships of the chromidotilapiines, *Pelmatochromis* and *Pterochromis*

The phyletic integrity of the chromidotilapiines seems well-established on the basis of various synapomorphic characters (see above). Two of those characters, the absence of microbranchiospines and the presence of a visor-like hanging pad in the pharynx, occur in other African cichlids. The phyletic significance of that fact cannot be properly evaluated in the present state of our knowledge about suprageneric affinities in the Cichlidae. What information we do possess certainly does not suggest a recent common ancestry for the taxa having those features. Rather it would suggest their repeated evolution in different lineages (see Greenwood, 1983).

Earlier suggestions that, through *Thysia*, the chromidotilapiines could be related to the *Hemichromis–Anomalochromis* lineage (see Loiselle & Welcomme, 1972) cannot be substantiated on the basis of uniquely shared apomorphies (see Greenwood, 1985*a* & *b*). The *Hemichromis–Anomalochromis* group is another of those cichlid lineages easily defined on the basis of its autapomorphic characters, but otherwise only showing a suite of widely occurring and plesiomorphic features which give no indication of its nearest relatives.

Outside the chromidotilapiines, *Pelmatochromis* provides a particularly intriguing phylogenetic puzzle. Although its supposed close relationship to the chromidotilapiines (Thys, 1968*a*) cannot be satisfactorily substantiated (see p. 192), its generalised oral dentition and the derived form of its gill-rakers would seem to favour the possibility of it being the plesiomorph sister taxon to that lineage (see above, p. 193).

In complete contrast to that possible relationship is the other suggestion put forward by Thys (1968*a* & *b*), that *Pelmatochromis* is closely related to, or even a member of the genus *Tilapia*.

Thys (1968*a*) expressed the view that *Pelmatochromis nigrofasciatus* (which he mistakenly identified as *P. ocellifer*; see Trewavas, 1973) and *Pterochromis congicus* (then included in *Pelmatochromis*) seemed to bridge the morphological gap between *Pelmatochromis* and *Tilapia*. He also included in that bridging group *Pelmatochromis ruweti*, a species now included, and properly so, in *Tilapia* (see Thys, 1968*a*). As a member of that genus, *T. ruweti* is excluded from the discussion which follows.

Reasons for considering *Pelmatochromis nigrofasciatus* and *Pterochromis congicus* being close to, or actually members of *Tilapia* are, according to Thys, the common possession of a *Tilapia*-spot

on the dorsal fin, the presence of microbranchiospines, lanceolate and not tuberculate gill-rakers, pointed pelvic fins in both sexes, 16 scales around the caudal peduncle, no hanging pad in the pharynx and '. . . all stages (with regards to mouth shape and dentition) of a gradual transition to *Tilapia sparrmanii*, type species of the genus *Tilapia* . . .' (Thys, 1968*a*: 369).

Of the characters he lists, all but the dentition and gill-rakers in both *Pelmatochromis* and *Pterochromis*, and the oral ones in *Pterochromis*, are plesiomorphic features and thus of no value in establishing relationships.

Jaw morphology in all three species of *Pelmatochromis* is very close to that in *Tilapia sparrmanii* (and other *Tilapia* species) and therefore cannot be considered as bridging the gap between the *Tilapia* condition and the far more extreme, predator-like one characterizing *Pterochromis* (see p. 155). Nor can I agree with Thys' comment on the gill-rakers as applied to *Pelmatochromis*. As has been frequently mentioned in this paper, the gill-rakers in that genus closely resemble those in the chromidotilapiines, and are quite unlike the relatively simple, near-vertically orientated structures in *T. sparrmanii* and indeed of other *Tilapia* species (the concept of *Tilapia* used here being that of Trewavas, 1983). Admittedly there is some resemblance between the gill-rakers of *Pterochromis congicus* and those of certain tilapiine species, but there are no other features to suggest either a close relationship between that species and any *Tilapia* or any *Pelmatochromis* species (see above, pp. 155–6).

Thus, the only characters which might be of relevance are the dental ones. Since the teeth of *Pterochromis* are all unicuspid and conical, and bear no resemblance to those occurring as the principal dental elements in any *Tilapia* species (see Trewavas, 1973: 12), *Pterochromis* can be dismissed immediately from this aspect of the discussion.

Trewavas (1973) deals at length with the presumed resemblances between *Pelmatochromis* and *Tilapia* teeth. From her survey she concluded that 'The only species of *Pelmatochromis* showing any evidence of derivation from an ancestor with a *Tilapia*-like dentition is *P. nigrofasciatus*. The fact that the teeth are notched only at such an early stage that they can hardly be functional as such suggests that they are a vestigial feature derived from an ancestor that had indeed a *Tilapia*-like dentition' (*op. cit.*: 19).

Broadly speaking, I would agree with Trewavas' views on the teeth being a vestigial feature, especially since there are traces of a bicuspid juvenile dentition in another *Pelmatochromis* species (see p. 145). But even though, in the present state of our knowledge, *P. nigrofasciatus* has the most clearly bicuspid juvenile teeth, I would not consider them to be strictly *Tilapia*-like in detail. Rather, I would consider that they share with those of *Tilapia* only the feature of a bicuspid crown. The shared possession of teeth with bicuspid crowns, however, is too vague a character to use critically when attempting to unravel phyletic relationships, the more so since simple bicuspid crowns would seem to be a primitive adult condition amongst African cichlids (Greenwood, 1979; 1980), and there are many and derived variants on the bicuspid theme.

In short, none of the features listed by Thys (1968*a*) would support either a conclusion that *Pelmatochromis* and *Pterochromis* be treated as members of the genus *Tilapia*, or that the two taxa are closely related to *Tilapia* and might be derived from a *Tilapia busumana* or *T. buttikoferi*-like ancestor as was suggested by Thys (1968*a*: 377).

Thys' suggestions led me to check carefully on the published diagnostic features for *Tilapia* and to examine in some detail specimens of *T. busumana, T. sparrmanii, T. ruweti* and *T. zilli*. The object of that study was not only to see if there are synapomorphic features shared by *Tilapia* and *Pelmatochromis*, but to find autapomorphic features which would define *Tilapia* and the group tilapiini as a whole (*sensu* Trewavas, 1983). Neither search proved successful.

Trewavas' (1983) detailed account of *Tilapia* in relation to its sister taxa *Oreochromis, Sarotherodon* and *Danakilia* provided only one synapomorphic feature for those genera, namely a long gut. The other derived features apparent from her account are autapomorphies for the various genera other than *Tilapia*, which seemingly has no defining autapomorphies, at least in its morphological characteristics. My studies on the cranial and pharyngobranchial anatomy of *Tilapia* also failed to produce a single autapomorphy.

One feature not previously noted, however, would seem to provide an additional synapomorphy for the tilapiines as a whole. Namely, the shape, in lateral profile, of those pharyngeal teeth situated

Fig. 30 Two 'kukri' shaped lower pharyngeal teeth from the anterior dental field in *Oreochromis variabilis*. Magnification × 100 (BMNH 1911.10.28:14).

in the anterior dental field of the lower pharyngeal bone. In the majority of cichlids, both African and Neotropical, these teeth are simple unicuspids or are clearly bicuspid. In either type, the tip of the cusp lies in the vertical passing through the body of the tooth or but slightly behind it. The tilapiines, however, have anterior field teeth with a very distinctive cusp form; the upper part of the tooth is angled posteriorly, and the vertical through its tip lies well behind the body of the tooth. When viewed laterally such teeth have an outline recalling the blade of a 'kukri', the Nepalese knife much favoured as a weapon by Gurkha soldiers (see Fig. 30). I have checked several species in each of Trewavas' (1983) tilapiine genera *Tilapia, Oreochromis, Sarotherodon*, and the monotypic *Danakilia* and *Iranocichla*, and find that 'kukri' teeth are present in all. Interestingly, none was recognizable in the endemic tilapiine genera of the Cameroonian lake Barombi Mbu (*Myaka,*

Konia, Stomatepia and *Pungu*), while in the Levantine *Tristramella*, teeth closely approaching the 'kukri' type are present, but apparently restricted to the posterolateral dental fields. 'Kukri' teeth do not occur in any of the pelmatochromine genera.

'Kukri'-shaped teeth, or teeth closely similar to them, also occur in at least some Lake Malawi species of the genus *Pseudotropheus*, for example, *P. tropheus, P. auritus* and *P. livingstoni* (not all species of this large genus were examined). That record, coupled with the general absence of 'kukri' teeth in other African and Neotropical taxa suggests that such teeth have evolved at least twice within the family since there is no evidence to suggest that *Pseudotropheus* and the tilapiines are closely related.

Another apomorphic feature in the pharyngeal jaws of all but one species of the *Tilapia, Oreochromis, Sarotherodon, Danakilia, Iranocichla* group, concerns the shape and spatial relationships of the upper pharyngeal bone (fused 3rd and 4th pharyngobranchials) of each side. Whereas in *Pelmatochromis, Pterochromis* and all the chromidotilapiines, as well as in the majority of African and Neotropical taxa, the two bones form a broad and shallow V (see p. 149, and Fig. 4A), in the tilapiine genera the bones are closely apposed along their medial faces, and together have a distinctly cardiform outline (Fig. 4B), one enhanced by their relatively broader and less ovoid toothed surfaces. The exceptional species is *Tilapia busumana*. Here the bones are narrower and form the generalized V-shape. *Tilapia busumana* is, of course, the species which Thys (1968*a*:377) indicated as being close to the stem of the pelmatochromine assemblage. Arguments for not accepting a close relationship between *Pelmatochromis* (or any pelmatochromine) and *Tilapia* have been given above, and are not affected by the two taxa sharing this plesiomorphic feature. That it is a plesiomorphy lost in, apparently, all other tilapiines, would, however, seem to indicate the possibility of *T. busumana* being a primitive tilapiine.

A cardiform arrangement of the upper pharyngeal bones is by no means confined to the tilapiine genera. It has been found in *Labrochromis* and *Astatoreochromis* from Lake Victoria, in *Tylochromis* and *Cardiopharynx* of Lake Tanganyika, in *Cyathochromis* and *Petrotilapia* from Lake Malawi, and in at least four Neotropical species as well. A condition approaching the cardiform one more closely than the V-shaped arrangement occurs in the supposedly primitive Asiatic *Etroplus oligacanthus* and in the Malagasian *Ptychochromis*. Arrangements intermediate between the cardiform and V-shaped types, but rather closer to the former, are found in *Simochromis* and *Xenotilapia* from Lake Tanganyika and *Paratilapia polleni* from Madagascar, and a reversed cardiform arrangement (with the 'auricular' part of the 'heart' directed anteriorly rather than towards the oesophagus) occurs in the Malagasian *Paretroplus dami*.

With such a range of variability, and of distantly related taxa in which the cardiform arrangement occurs, it would seem to be a feature which has evolved several times, and independently, within the Cichlidae, including some of its members generally accepted as having a plesiomorphic level of organization (e.g. *Tylochromis* and the etroplines of Asia and Madagascar). That it is an apomorphic feature seems probable from its absence in other labroids and in the percoid outgroups examined.

In the majority of species with a cardiform arrangement, the teeth of the upper pharyngeal bones are either enlarged and molariform, or fine, numerous and densely packed, a situation which may be correlated with the bones themselves having a larger surface area relative to the subovoid bones associated with the typical V-shaped arrangement.

The absence of 'kukri'-shaped teeth on the lower pharyngeal bones, and the persistence of the plesiomorphic V arrangement of the upper pharyngeal elements in all pelmatochromine taxa, provide yet other reasons for refuting the idea that *Pelmatochromis* and *Pterochromis* are members of the tribe Tilapiini *sensu* Trewavas (1983). That assemblage besides *Pelmatochromis* and *Pterochromis*, contains the genera *Tilapia, Oreochromis, Sarotherodon, Danakilia, Iranocichla, Tristramella*, the endemic genera of Barombi Mbu, and possibly *Steatocranus* and *Gobiochromis*. Its only unifying group-character cited is the *Tilapia*-type apophysis, which as Trewavas (*op. cit.* and 1986) recognises, is plesiomorphic for the cichlids. As such it cannot be used to establish the monophyly of the Tilapiini (see also Greenwood, 1978, and 1987).

Establishing the monophyly of Trewavas' Tilapiini, even after the removal of *Pelmatochromis* and *Pterochromis*, is a task that remains to be done. The use of upper pharyngeal bone arrange-

ment, and the presence of 'kukri'-shaped teeth may prove of some value in that task, but neither feature can yet be considered a fully corroborated synapomorphy for the group.

Of the two taxa which can be eliminated from the Tilapiini, *Pelmatochromis* may be the plesiomorph sister taxon to all the chromidotilapiines (see p. 192), but the relationships of *Pterochromis* are at present unknown (see p. 192). Its principal diagnostic phenotypic characters are all autapomorphic ones that could be derived, by differential growth, from a *Pelmatochromis*-like ancestor which did not have the derived gill-raker morphology of the extant *Pelmatochromis* species. Other changes from such a presumed ancestor would involve slight modifications to the detention and dental patterns.

All that is speculation, and a reflection of the fact that such a proto-*Pelmatochromis* could well provide a morphotype from which a number of extant lineages, including *Tilapia* and its close relatives, evolved. If that is so, their unifying synapomorphies have still to be identified.

In conclusion, what can be said about the intrafamilial relationships of chromidotilapiines, *Pelmatochromis* and *Pterochromis*? In a positive sense, the answer must be 'Nothing'. Previously suggested relationships can be refuted, and one is left with a number of apparently monophyletic lineages whose relationships at higher phyletic levels are presently indeterminable.

The distribution of *Pterochromis, Pelmatochromis* and the chromidotilapiines

The chromidotilapiines as a whole (*Thysia, Chromidotilapia, Pelvicachromis, Limbochromis, Parananochromis* and *Nanochromis*) have a fairly extensive latitudinal range from about 10°N to 5°S. They are, however, with the exception of *Nanochromis* and one *Chromidotilapia* species, confined to a relatively narrow strip, some 200–300 miles wide, extending along the western margin of Africa. This strip lies mainly within the lowland forest zone, but in places it extends into the areas of moist woodlands and savannah. The range of *Nanochromis*, however, extends further eastwards into the central regions of the Zaire river and its tributaries, although the greater number of its species is found in the fast-flowing waters of the river's lower reaches. The exceptional *Chromidotilapia* species, *C. schoutedeni* occurs outside the marginal zone and is found in the lower parts of the Lualaba river.

Pelmatochromis has a wide but scattered distribution which includes the central Zaire area, Senegal, Guinea, Liberia and Sierra Leone, while *Pterochromis* is apparently restricted to Central Zaire in the region of Kisingani. For detailed distributions of the various species see Thys, 1968*a*; Thys & Loiselle, 1971; Loiselle & Welcomme, 1972; Trewavas, 1973 and 1974; Roberts & Stewart, 1976; Linke & Staeck, 1981; Stewart & Roberts, 1984.

There is remarkably little distributional overlap between the chromidotilapiines, *Pelmatochromis* and *Pterochromis* on the one hand, and any of the non-tilapiine fluviatile species of eastern and middle Africa on the other. The non-tilapiine species in question are represented by members of the haplochromine genera *Astatotilapia, Ctenochromis, Thoracochromis, Astatoreochromis* and *Orthochromis* (see Greenwood, 1979).

In geographical terms, and to a certain extent in their trophic specializations as well, the chromidotilapiines, plus *Pelmatochromis* and *Pterochromis*, together with *Hemichromis* and *Anomalochromis* (see Greenwood, 1985*a* & *b*) seem to be the far western equivalents, and ecological counterparts, of the eastern haplochromines mentioned above. It is, of course, difficult to quantify degrees of morphological differentiation, but the two geographical entities seem to have evolved and differentiated to about the same extent. A noticeable difference, however, is the absence of any far western species in which the pharyngeal mill is hypertrophied. Indeed, the morphological details involved in the differentiation of the two groups are generally quite different. For example, no eastern species has evolved a dentition like that in the chromidotilapiines, none has a visor-like hanging pad in the pharynx, none has gill-rakers with the complex form of those in the chromidotilapiines, and all have retained microbranchiospines. However, in superficial features the eastern and western rheophilic taxa, *Orthochromis* and *Nanochromis* respectively, are, perhaps not unexpectedly, remarkably similar.

Summary and conclusions

The pelmatochromine cichlids (*sensu* Thys, 1968*a*) of western Africa can be divided into a monophyletic lineage (informally categorized as the chromidotilapiines) comprising the genera *Thysia, Chromidotilapia, Pelvicachromis, Nanochromis, Parananochromis* and *Limbochromis* (the two latter genera described in this paper), and two other monophyletic taxa, *Pelmatochromis* and *Pterochromis.*

The intrarelationships of the chromidotilapiines cannot be satisfactorily resolved; it is suggested that *Thysia* is the plesiomorphic sister taxon to the other five genera combined, and that within this combination *Parananochromis* and *Nanochromis* are sister genera, and are the most derived members of the chromidotilapiines.

There are indications that two of the chromidotilapiine genera, although monophyletic assemblages themselves, should be subdivided. In *Nanochromis*, for example, one group of species has the posterior half of the upper lateral-line in contact with the dorsal fin base, whilst in the other, only the last four or five scales of the lateral-line are contiguous with the fin base. In *Pelvicachromis, P. humilis* shows certain derived features which suggest that it may represent an off-shoot of the main species assemblage. Both these problems may be clarified when more material is available, and further anatomical and osteological studies can be made. Ethological and other aspects of the species' natural history may also prove of great value in unravelling the still outstanding problems.

Although *Pelmatochromis* apparently shares one derived character, the nature of its gill-rakers, with the chromidotilapiines, no further and congruent synapomorphies could be discovered to support its possible sister-group relationship with those species. Equally, the absence of other derived features in *Pelmatochromis* does not give any indication of other taxa to which it might be related.

Pterochromis exhibits several autapomorphic features but, like *Pelmatochromis*, it seems to show no derived features positively indicative of its relationships within the family.

The suggestion (Thys, 1968*a* & *b*) that *Pelmatochromis* might be closely related to, or even a member of the genus *Tilapia* is reexamined and found to be untenable both for the reasons given by Trewavas (1973) and on the basis of other characters as well. Its suggested membership of a tribe containing *Tilapia, Oreochromis, Sarotherodon* and several other genera (see Trewavas, 1983) is also rejected. In that connection, the phylogenetic basis (as opposed to one based on overall similarity) of the Tilapiini is reconsidered. Two possibly apomorphic characters, for at least some members of the tribe, are identified; neither is present in any of the pelmatochromine taxa, thus providing further evidence against their possible close relationship with *Tilapia.*

Neither the chromidotilapiines nor *Pelmatochromis* and *Pterochromis* are closely related to any of the fluviatile haplochromine lineages from eastern Africa, and there is very little geographical overlap between the two groups. The essentially far western distribution of the chromidotilapiines, *Pelmatochromis* and *Pterochromis* contrasts strongly with the wider geographical distribution of the eastern haplochromine lineages (see above, p. 199, and Greenwood, 1979).

Like the various haplochromine lineages of Lake Victoria (see Greenwood, 1981; 1984), the chromidotilapiines exhibit a gradual trend in the evolution of certain morphological characters, with each stage in the morphocline represented by one or several species. Amongst the Lake Victoria haplochromines this display of cladistic gradualism principally involves trophic specialization. In the chromidotilapiines it involves traits associated with an increasingly rheophilic way of life. Little is known about the feeding habits of the chromidotilapiines but judging from the oral and pharyngeal dentition, and from associated structures, there is probably little intragroup trophic specialization and differentiation.

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British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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Synopsis

Thirteen species of sea-anemone from the tropical Red Sea and the Indo-Pacific Ocean are described in detail and notes are given on a further three. Certain taxonomic characters are discussed, marginal spherules are re-defined and the concept 'nematocyst signature' is introduced. The genus *Edwardsia* de Quatrefages, 1841, is revised. Details of two nematocyst types found in the nemathybomes are given, newly designated pterotrich and microbasic t-mastigophore. The genus *Edwardsioides* Danielssen, 1890, is re-established and the related genus *Edwardsianthus* nov. introduced. Descriptions are given of *Edwardsia hantuensis* sp. nov., *Edwardsianthus pudica* (Klunzinger, 1877) comb. nov., and *Scolanthus armatus* (Carlgren, 1931) comb. nov.

Triactis producta Klunzinger, 1877 (Aliciidae) is redescribed. Descriptions are given of the actiniid species *Anthopleura dixoniana* (Haddon & Shackleton, 1893), *A. handi* Dunn, 1977, *A. nigrescens* (Verrill, 1928), and *A. waridi* (Carlgren, 1900). The genus *Gyractis* Boveri, 1893, is re-established to accommodate the species *G. excavata* Boveri, 1893, and its relation to *Aulactinia* Verrill, 1864, is discussed. Three new genera are proposed in the Actiniidae: *Mesactinia* gen. nov., *Neocondylactis* gen. nov. and *Telactinia* gen. nov.; and the included species *Telactinia citrina* (Haddon & Shackleton, 1893) comb. nov., *Mesactinia ganensis* sp. nov. and *Neocondylactis singaporensis* sp. nov. are described. The scope of the family Stichodactylidae is widened to include the genus *Entacmaea* Ehrenberg, 1834; and the genus *Antheopsis* Carlgren, 1900, is reinstated. New information is given on the species *Entacmaea quadricolor* Rueppell & Leuckart, 1828, and *Antheopsis malayensis* sp. nov. is described. The date of Carlgren's definition of the family Hormathiidae is discussed. A note is given on the inclusion of the conspecific *Actinia decorata* (Dana, 1846) with *Calliactis polypus* (Forsskål, 1775).

The three species *Carcinactis dolosa* Riemann-Zürneck, 1975, *Carcinactis ichikawai* Uchida, 1960, and *Verrillactis paguri* (Verrill, 1969*a*) are compared.

Type designations

Type material is designated of the nominal species *Antheopsis malayensis* sp. nov. (p. 274), *Edwardsia hantuensis* sp. nov. (p. 221), *Mesactinia ganensis* gen. nov., sp. nov. (p. 263) and *Neocondylactis singaporensis* gen. nov., sp., nov. (p. 265).

Priapus polypus Forsskål, 1775, is designated type species of the genus *Calliactis* Verrill, 1969*b* (p. 279), family Hormathiidae.

Type species are designated of the genera *Edwardsianthus* gen. nov. (p. 224) and *Edwardsioides* Danielssen, 1890 (p. 224), family Edwardsiidae; *Mesactinia* gen. nov. (p. 261), *Neocondylactis* gen. nov. (p. 265) and *Telactinia* gen. nov. (p. 268), family Actiniidae.

Introduction

Little taxonomic work on tropical sea-anemones has been published since Carlgren's (1950*a*,*b*) papers on the Actiniaria and Corallimorpharia of the Great Barrier Reef, South Queensland and New South Wales. The only substantial publication since 1950 has been that of Dunn (1981) on the clownfish sea-anemones. The opportunity was taken, during military service, to collect Actiniaria and Corallimorpharia from a variety of tropical and sub-tropical sites; in Aden and Bahrain in 1966; in Gan, Addu Atoll, Maldives, in 1970 and 1971; and in Singapore and Malaysia (Penang and Pulau Tioman) from 1969 to 1972. The collection comprised some 50 species of which 13 are

described here and notes on a further 3 included. In addition numerous locality records of anemones not treated taxonomically are included. The study was augmented by material from the British Museum (Natural History) and specimens kindly made available by others from Sri Lanka, Hawaii, the Tuamoto Isles, Hong Kong, Madagascar and Egypt. The new material has been deposited in the British Museum (Natural History).

Methods

The collecting sites are described according to habitat. A species list from each habitat is given. Not all the species found are described in this paper, but lists of them are included to show the wide variety that occurred in these areas and to provide faunal records. In the areas investigated four distinct habitats were studied as follows.

(a) Mangrove swamp. Here Actiniaria and Corallimorpharia were absent, although Stephenson, Stephenson & Tandy (1931: 38) recorded some specimens from a pool near the mangroves of Low Isles in the Great Barrier Reef. Mangrove areas were examined in Singapore and around Pulau Tioman, Malaysia.

(b) Intertidal mud with occasional rocks, but not associated with mangroves. In Aden, near the Causeway below Jebel Hadid, one such area was rich in actiniarians. They included *Edwardsianthus pudica* (Klunzinger, 1877), comb. nov., *Antheopsis koseirensis* (Klunzinger, 1877), *Stichodactyla gigantea* (Forsskål, 1775), *Heteranthus verraculatis* Klunzinger, 1877, found in the mud, and *Aiptasia* sp., *Anthopleura stellula* (Ehrenberg, 1834) and *Haliplanella luciae* (Verrill, 1898) found on small stones, pieces of rope and an old oil drum. Large numbers of hermit crabs (species not determined) were found in this area, possibly attracted by fishermen's offal, but the crabs never had associated symbiotic anemones. Other Cnidaria observed included *Cassiopeia* sp. (Scyphozoa), *Cladonema* sp. (Hydrozoa: hydroid stage), and a large cerianthid.

At Singapore several similar areas occurred on the northern coast, including Pungol Point and Pasir Ris which were examined. Numerous specimens of *Actinothoe* sp. were found on several different species of *Nassarius* spp. (Gastropoda), and *Neocondylactis singaporensis* gen. nov. sp. nov., *Scolanthus armatus* (Carlgren, 1931) and a large cerianthid were observed in the mud. *Anthopleura dixoniana* (Haddon & Shackleton, 1893) comb. nov. was found in small holes in an outcrop of yellow sandstone at Pungol Point and on stones of a broken wall at Pasir Ris, both locations being at Mean High Tide Level. Another muddy habitat at Singapore was an area which has now been reclaimed at Bedok. From here were collected specimens of *Paracondylactis* sp., *Sagartianthus* sp. associated with the crab *Diogenes diogenes*, and *Stichodactyla gigantea* (Forsskål, 1775). On the south coast of Pasir Panjang and Buona Vista was a diverse area of mud, sand and gravel with patches of the green alga *Halophila ovalis*. Here was again found *Actinothoe* sp. on *Nassarius* spp., and also *Edwardsia hantuensis* sp. nov., *Stichodactyla gigantea* (one large and several small specimens with symbiotic shrimp), and a cerianthid.

(c) Fringing coral reefs. Three zones were recognized:

1. The reef flat, usually comprising coarse sand with occasional rocks and coral heads.
2. The reef edge, an area extending back from the outer edge for some ten metres. This area comprised coral debris and sand with large coral heads and occasional hard rock, especially where wave action was high. Shelter from wave action was associated with growth of many living corals and algae.
3. The reef slope, fairly steep and comprised entirely of coral debris, which continued down to depths of more than thirty metres around the islands off Singapore and to greater depths in parts of the reefs at Gan and elsewhere. In other localities it consisted of rocks covered with many species of corals and occasional actinians.

On the reef flats surrounding the Singapore islands, particularly Pulau Hantu, the following species were noted in the sand: *Actinodendron* sp., *Edwardsianthus pudica* comb. nov., *Metapeachia tropica* (Panikkar, 1939), *Scolanthus armatus* comb. nov., *Stichodactyla gigantea*, *S. kenti* (Haddon

& Shackleton, 1893), and several species of Discosomatidae. On the Cyrene Reef, however, the reef flat was covered with *S. kenti*. On Gan, from similar habitats on the reefs inside the lagoon, *E. pudica*, *S. kenti* and *Rhodactis* sp. were recorded. At the reef edge the number of species was correlated with the amount of wave action. If the edge was composed only of rock and was subject to heavy wave action few actinians or corallimorpharians were present. In Gan the only species found was *Gyractis excavata* Boveri, 1893, inhabiting cracks and crevices in extremely hard rock, but in Aden it was associated in such places with *Phymanthus loligo* (Ehrenberg, 1834). *Gyractis excavata* has been recorded from similar locations in Hawaii (as *Actiniogeton sesere* by Dunn, 1974*b*: 181–188) and Fiji (J.S. Ryland, personal communication). Where wave action was low, as at Singapore and inside the lagoon of Gan, the reef edge was composed of living coral and sand. Many actinians occurred here, attached to coral stems above or below the sand. *Edwardsianthus pudica* comb. nov., *Radianthus malu* (Haddon & Shackleton, 1893), *Phymanthus muscosus* Haddon & Shackleton, 1893, and a cerianthid occurred in the sand. Among the corals and attached to their stems were *Cryptodendron adhaesivium* Klunzinger, 1877, *Entacmaea quadricolor* (Rueppell & Leuckart, 1828), *Telactinia citrina* comb. nov.; and the corallimorpharians *Rhodactis bryoides* (Haddon & Shackleton, 1893), *R. rhodostoma* (Ehrenberg, 1834), *Metarhodactis boninensis* Carlgren, 1943, and *Ricordea yuma* (Carlgren, 1900).

Reef slopes composed of rock were usually covered with corals, and few actinians were seen. This was so at Gan where no actinians were found during several dives made in the area. The only anemone seen was on the wreck of the oil tanker *British Loyalty*. If the reef slope consisted of coral debris the surface was mobile preventing animals retaining a hold, and few animals of any species were found. At the foot of such reef slopes, at 30–40 m depth, specimens of *Radianthus malu* and *R. macrodactyla* (Haddon & Shackleton, 1893) were occasionally found, but their small number suggests that they may have been displaced from the reef edge. In some areas of Pulau Hantu and Pulau Tioman, outcrops of rock occurred on the reef slope with the tops just below Mean Low Water Springs (MLWS). These locations seemed favoured by *Radianthus magnifica* (Quoy & Gaimard, 1833).

In coral areas that had been devastated by storms, human activity, or the starfish *Acanthaster planci* (Linnaeus, 1758), it was observed that the area was first reoccupied by *Rhodactis* sp. This corallimorpharian appeared to colonize rapidly and large areas covering many square metres were soon carpeted. This was noted at Pulau Tioman and again in Gan where the reef corals alongside the jetty had been destroyed by abrasion by ships at low water.

(d) Rocky areas, not associated with reefs. In the intertidal zone these were the habitat for *Aiptasia* sp., *Anthopleura dixoniana*, *A. stellula* and *A. waridi* (Carlgren, 1900) comb. nov.; and also for *Corynactis* sp. In deeper waters actinians were found also on antipatharians: for example, several specimens of *Nemanthus* sp. were found on the main stems of black corals in Pulau Tioman.

Around Singapore Islands there were many specimens of gorgonians and whip corals at depths between 4 and 40 metres. Despite prolonged searching no actinians were found on them.

Collection. Specimens were removed with the substrate to which they were attached or were prised carefully from it. Attempts to loosen specimens from the substrate by chemical means rarely worked, the anemones closing up tightly and remaining strongly attached. Soda water and weak solutions of formaldehyde and bleach were tried unsuccessfully.

With burrowing anemones such as *Edwardsianthus* spp. and cerianthids it was found most effective to dig gently downwards to a depth of 40–50 cm but 30–40 cm away from the animal and then to tunnel underneath it before attempting capture. It was not uncommon to lose a specimen, since when disturbed most burrowing species contract rapidly and move downwards.

Preservation. Specimens were narcotized in 3·5–4·0% $MgSO_4.7H_2O$ in sea water. In the field this was not always possible so $MgSO_4$ crystals were added to a vessel of sea water containing the specimen. With small specimens 30 minutes was adequate for narcotization, but larger specimens were left overnight and some were still not completely narcotized by morning. For large specimens, menthol or a combination of menthol and $MgSO_4$ was also used overnight. When an anemone had

lost tactile sensitivity 40% formaldehyde solution was injected from a pipette or hypodermic syringe into the enteron via the mouth, care being taken to avoid inflating it. 10% formaldehyde solution was then sprayed from a pipette over the outside of the specimen. Finally it was transferred to a fresh container containing 10% formaldehyde-sea water solution and labelled. Specimens were transferred to 70% C_2H_5OH later on. Storage in formaldehyde-sea water solution for prolonged periods sometimes hinders subsequent staining and the tissues may start to macerate.

Other methods of killing and preserving specimens have been used (Lee, 1921: 521), but not always successfully. The use of hot Bouin's fluid on specimens of *Anthopleura waridi* resulted in the ectoderm becoming detached, with consequent loss of the nematocysts from the spherules at the margin and in the fosse, and this led to an incorrect determination (England, 1969: 5).

Corallimorpharians, such as *Rhodactis rhodostoma*, were the most difficult to preserve, since they exuded mucus when chemicals were added to the water to narcotize them. The mucus not only prevented narcotization but seemed to hinder fixation of the tissue by formaldehyde, especially internally. Fixing in 70% C_2H_5OH overcame the difficulty but the specimens tended to be badly contracted. Glutaraldehyde was used with good results.

Examination of material. Specimens were examined with a dissecting microscope under alcohol. At this stage it was useful to stain some of the smaller species in bulk with borax carmine to facilitate the observation of certain features, such as sphincter muscles, micro-mesenteries and suckers on the column if present. Alcoholic picro-indigo-carmine was found a better stain than borax carmine for showing micro-mesenteries that hardly break the surface of the endoderm, and which would normally be detected only be means of serial sections. If it was desired to remove this stain differentiation in 70% C_2H_5OH was used. Continued changes of 70% C_2H_5OH removed the stain completely from most specimens, but occasionally picro-indigo-carmine became permanent, depending perhaps on the method of fixation. Alternatively, if acid alcohol (0·5% HCl, 70% C_2H_5OH) was used the stain was both differentiated and fixed. This method of bulk staining greatly reduced the need for cutting sections.

If sections were required selected pieces of the specimen were removed and stained with borax carmine (unless already stained). Histological sections were cleared in cedarwood oil or terpineol and embedded in paraffin wax (m. pt. 55–57°C) or Fibrowax (m. pt. 57°C). Double embedding in celloidin and Fibrowax was also employed. 10 μm sections were cut using a Cambridge rocking microtome. Most of the sections were counter-stained with picro-indigo-carmine (Stephenson, 1928: 55–56), but other staining methods used included Ehrlich's haematoxylin and eosin, and Mallory's triple stain (Peacock, 1966: 421 & 441). Drawings prepared from the stained sections were made without the aid of a camera lucida. Where part of an illustration was left blank it was because the specimen was inadequate at that point (Figs 3d, 10b). Where an illustration is intended to be diagrammatic this is stated.

Nematocysts. Squash preparations were made of small portions of preserved tissue, approximately 1 mm^2, from tentacles, column, actinopharynx and filaments, and also from acontia, spherules, nemathybomes and vesicles, when present, to identify the types of nematocyst and to measure them. The samples taken from tentacles, column and actinophrynx were obtained by scraping off ectoderm: this avoided contamination with nematocysts from the endodermal epithelium or filaments, or from acontia which, when present, frequently extended from the enteron into the tentacles. The selected tissue was treated with 2% aqueous $KMnO_4$ on a slide for 2 minutes, the solution removed with filter paper and a drop of glycerine placed on the tissue. It was then teased and afterwards gently squashed under a coverslip by finger pressure using a little sideways movement. It was necessary to exert only gentle pressure at this stage, before examining the preparations to identify the types of nematocyst present. Large holotrichs and spirocysts were easily damaged or completely destroyed if too much pressure had been applied or too much sideways motion given to the coverslip. It was at this stage still possible to see the nematocysts *in situ* in the tissue and to confirm their presence in that position. When only a few nematocysts occurred in certain positions it was sometimes difficult to be certain that they belonged there and were not contaminants from

elsewhere. When doubt existed serial sections were examined to confirm their true location. After the types of nematocyst had been determined and any large, easily damaged nematocysts measured, the preparation was subjected to further squashing to break up the tissue surrounding the nematocysts. The majority of nematocysts were thereby clearly displayed, mostly lying flat. Three separate slides of the tissue from each location were examined. Sometimes replicate preparations were stained with 1% methylene blue or 1% acid fuchsin. Methylene blue stains atrichs, basitrichs and heterotrichs intensely so that they stand out from the surrounding tissue, but the capsular contents cannot be seen. If basitrichs and atrichs of a similar size range occurred in the same piece of tissue it would not be possible to separate them under these conditions. For general work and identification of the capsular contents of undischarged nematocysts staining with $KMnO_4$ was best. The $KMnO_4$ partially macerated the tissue but did not damage the nematocysts or alter their size. When the nematocyst contents remained indistinct after staining, identification was achieved using a 100x phase contrast objective.

Each preparation was scanned under oil immersion and the largest and smallest capsules of each undischarged nematocyst type were observed and measured ($\pm 0{\cdot}5$ μm) with an eyepiece micrometer. It was usual to measure 20–30 capsules of each type from three slides, and the size ranges reported here summarize these measurements. If fewer than 10 nematocysts were found altogether, the number seen was recorded as well as their size range (see Tables).

Terminology. The nematocyst nomenclature of Weill (1934) as modified by Carlgren (1940*a*: 3–4) has been used. Each nematocyst type is illustrated under each species. In addition two types of nematocyst originally noted by Carlgren (1940*a*: 23), the pterotrich and microbasic t-mastigophore, are redescribed and named (p. 219–221).

To describe the anatomy and structure of sea-anemones the terminology of Stephenson (1928, 1935) has been used throughout, though modified in places (see below).

Reappraisal of certain taxonomic characters

Marginal spherules. All blister-shaped protuberances occurring on the margin or in the fosse are termed spherules in this work (Fig. 1).

Since they include all three layers of the body wall they are similar in structure to verrucae but the ectoderm in this case is non-adhesive. Some spherules bear verrucae or adhesive spots on their outer faces. Spherules may have a battery of densely packed specific nematocysts, or they may have only a few nematocysts of the same types and size ranges as elsewhere in the column. A nematocyst battery, when present, is an addition to the spherule and often stands out from it, either as a cap completely covering it or as a small projection easily seen in both live and preserved material (Fig. 1a, c-e). Spherules showing this extent of variation, together with spherules devoid of nematocyst batteries, can occur with a single specimen, for example in *Anthopleura handi* (p. 245).

Many protuberances are armed with a large battery of atrichs and in the literature have been termed either acrorhagi or spherules, but if the battery of nematocysts is absent they have been called pseudo-acrorhagi or pseudo-spherules. The term acrorhagi was proposed by Andres, 1883: 283. Kwietniewski used the term 'Randblaschen' (1897*b*: 33), and others the term 'Randsackchen' (alternatively spelt 'Randsacken') (Lager, 1911: 219). Haddon, Kwietniewski and Lager appear each to have used these terms for both acrorhagi and pseudo-acrorhagi, so that it is not clear to which genus many of the species they described are best referred. It is now considered that acrorhagi are found, for example, in *Actinia*, *Anemonia*, *Anthopleura* and *Oulactis*, while pseudo-acrorhagi are found in *Paracondylactis*, *Gyractis* and in some other genera.

Some sea-anemones have marginal spherules which instead of atrichs possess large numbers of nematocysts of other types. *Telactinia citrina* comb. nov., and to a lesser extent *Mesactinia* gen. nov., for example, have large batteries of basitrichs (see p. 263, 270). Again, *Triactis* has spherules both in the fosse and on marginal peduncles armed with micro- and macrobasic amastigophores. The term acrorhagus is no longer useful because it includes at least three varieties of spherule for which precise terms are needed and it is not used in this account. Also, the term pseudo-acrorhagus

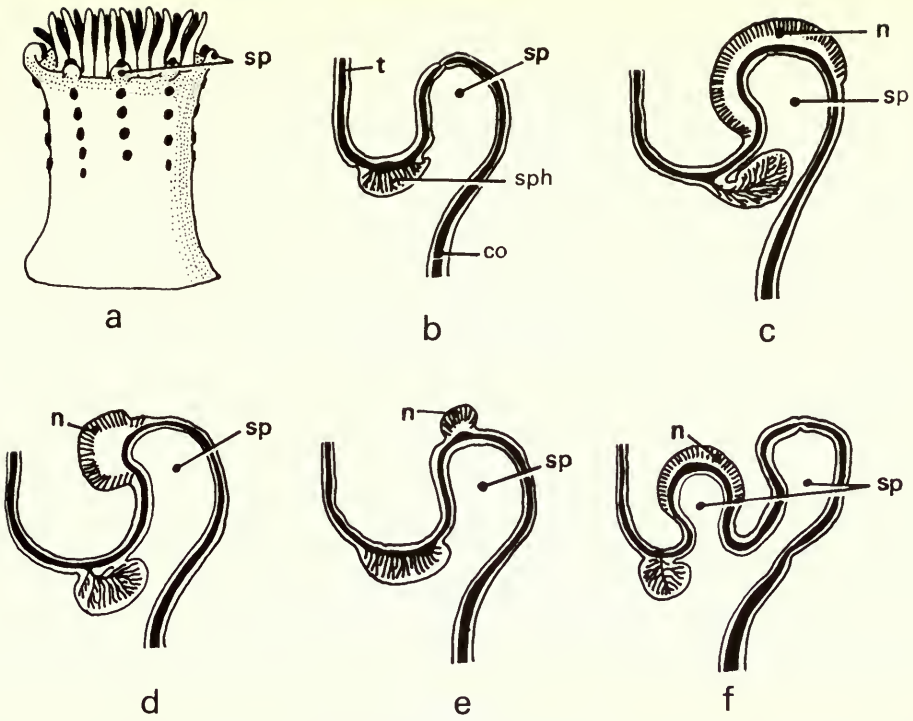

Fig. 1 Variation in marginal spherules (diagrammatic). (a) Typical appearance of *Anthopleura* sp. with large atrichal marginal spherules. (b) A marginal spherule lacking a nematocyst battery. (c) An atrichal marginal spherule completely capped by a nematocyst battery. (d) An atrichal marginal spherule with a small nematocyst battery, bent into the fosse. (e) Same, but upright. (f) Marginal spherule (to right) without a nematocyst battery but with an atrichal spherule in the fosse (as in *Anthopleura waridi*). (co column, n nematocyst battery, sp spherule, sph sphincter, t tentacle.)

(pseudo-spherule) is a misnomer in that a spherule is always present, whether it has a battery of nematocysts or not.

It is proposed that the term acrorhagus be dropped in favour of spherule. When spherules are specialized by the presence of specific nematocysts in a definite battery they can be classified as follows:

a. spherules armed with atrichs	Atrichal spherules
b. spherules armed with basitrichs	Basitrichal spherules
c. spherules armed with micro- and macrobasic mastigophores	Mastigophoral spherules

The position of a spherule can be on the margin, in the fosse or on the column. A full designation of a spherule of an *Anthopleura* specimen might be 'atrichal marginal spherule', or of one of *Actinia* 'atrichal spherule in the fosse'. Spherules are often armed with more than one type of nematocyst so the name applied is that of the more important or most numerous nematocyst present.

The term 'nematosphere', used to described the bunches of spherules on stalks between the tentacles of *Heterodactyla hemprichi* Ehrenberg, 1834, is retained.

Sphincter muscle. The type of sphincter has been used as a taxonomic character in the tribe Thenaria at various levels, for example:

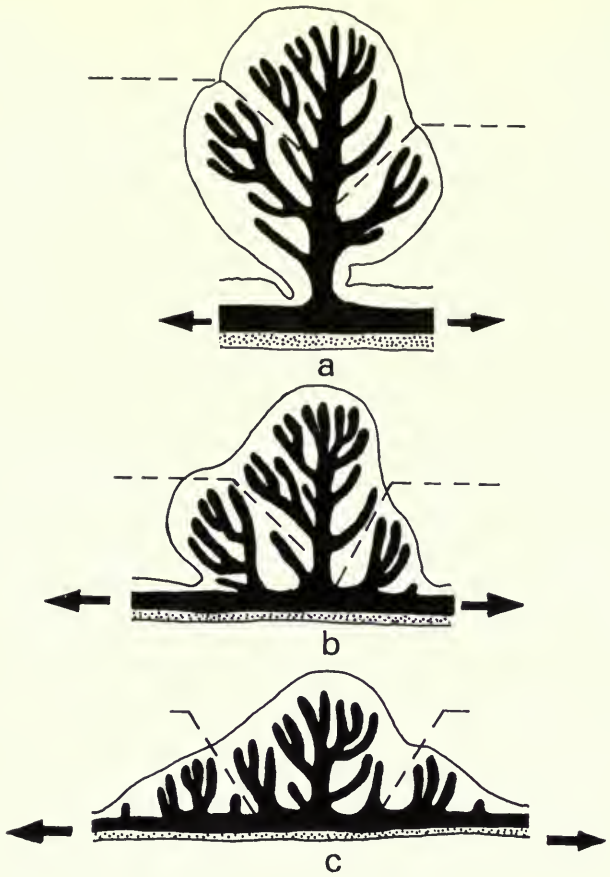

Fig. 2 Variation within a single sphincter due to state of expansion of the crown (diagrammatic). (a) A typical 'circumscribed-pinnate' sphincter. (b) A 'circumscribed-diffuse' sphincter (c) A 'diffuse' sphincter. Arrows indicate directions of expansion, dashed lines divide the sphincter into its elements. (Stippled, endoderm; black, mesogloea; white, endoderm.)

Subtribe level	Genera with endodermal sphincter	Endomyaria
	Genera with mesogloeal sphincter	Mesomyaria
Genus level	To separate genera that might otherwise form one large genus, for example in the Actiniidae:	
	Sphincter circumscribed	*Epiactis*
	Sphincter diffuse	*Entacmaea*
	Sphincter absent	*Phialoba*
Species level	The presence of a strong or a weak sphincter may be used to distinguish species	

In some species the sphincter is consistently of the same type, and unless the specimen is extremely distorted it is of uniform appearance in transverse section. In other species variation is observed as shown below in *Anthopleura dixoniana* (Fig. 18) and *Gyractis excavata* (Fig. 27). The sphincter of *A. dixoniana* varies from circumscribed to diffuse even within a single specimen.

The size and appearance of a sphincter can also differ within a species between one group or colony of individuals and another. Haddon was unaware of this when he proposed two species separated on this character, *Actinioides dixoniana* and *A. papuensis*, of which only one proved valid.

The appearance of a sphincter in transverse section depends on its degree of contraction and on the state of expanison of the crown (Fig. 2). As the crown expands its circumference increases and some mesogloeal folds of the sphincter are drawn outwards into the mesogloea of the margin. When a circumscribed sphincter is involved its main stem (see Fig. 2a) becomes assimilated and the branched folds spread out and become smaller until in the extreme case they are assimilated into the body wall. A striking example of this was seen in an Australian species *Epiactis australiensis* Carlgren, 1950*c* (Fig. 3). The first sections examined, cut parallel with the directive axis, appeared to have several separate sphincters (Fig. 3a), one large and four small. A transverse section taken at an angle of 45° to the first showed some of the smaller sphincters coalescing with the main muscle (Fig. 3b). A section cut at 90° to the directive axis showed all the smaller sphincters absorbed into the main muscle (Fig. 3c). A further change was seen at the next 45° position where the muscle passed through the mesentery (Fig. 3d). The muscle folds have not been drawn since they were completely anastomosed with those of the mesentery, but there were three separate sphincters.

Variation in the appearance of a single sphincter muscle around the margin due to local differences in its degree of contraction suggests that apparently different types of sphincter may prove to be the same. Figure 2 shows how a circumscribed sphincter transforms into a diffuse one. If the circumscribed sphincter is divided into its elements or mesogloeal folds, as indicated by the dashed lines in Figure 2a, the individual parts can be identified in the so-called diffuse sphincter (Fig. 2c). When this model is applied to the sphincters of *Anthopleura dixoniana* (Fig. 18) and *Gyractis excavata* (Fig. 27), each species is shown to have a sphincter which assumes several facies in transverse sections. Similar variation in the sphincter musculature is found in many other species, as for example in *Anthopleura nigrescens* (Fig. 22) and *Mesactinia ganensis* gen. nov., sp. nov. (Fig. 29). If the model in Figure 2 is applied, however, the sphincter muscles can be used at least at species level as a taxonomic character.

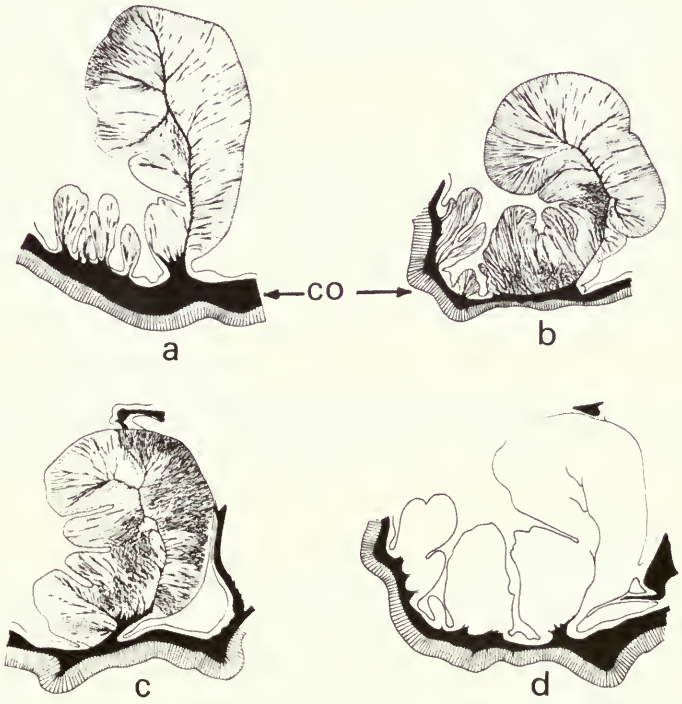

Fig. 3 *Epiactis australiensis*. Vertical sections showing variation of the sphincter in one specimen due to expansion of the crown. (a) At the directive axis, (b) at 45 degrees to the directive axis, (c) at 90 degrees to the directive axis and (d) at 45 degrees to the directive axis where the sphincter passes through the mesentery. (Hatched, ectoderm; black, mesogloea; white, endoderm; co column.)

Mesenterial arrangement. The relation of the number of tentacles, and hence of the number of mesenteries at the disk, to the number of mesenteries at the base is considered to be of generic importance. Three categories are recognized:

a. more mesenteries proximally than distally
b. same number of mesenteries distally as proximally
c. more mesenteries distally than proximally

These categories appear to be clear cut but in practice they intergrade. The mesenteries may develop from the base upwards, as for example in some species of *Anthopleura*, so that there are a few more at the base than at the margin. The reverse is also true, when tentacles and the corresponding mesenteries appear at the margin and grow downwards, as in *Mesactinia ganensis* gen. nov., sp. nov. It is also possible for mesenteries to appear at margin and base simultaneously and grow towards the centre of the column. An equal number of mesenteries may occur distally and proximally in juveniles but later on the number of mesenteries at the base might increase more rapidly than the number of tentacles, resulting finally in a difference of a complete cycle. Some species of sea-anemone have very small mesenteries at the margin and/or at the base, where they are little more than gussets of tissue as for example the microcnemes of *Edwardsia*. Among acontiate anemones *Calliactis polypus* (see England 1971: 25) may have minute mesenteries at both margin and limbus, but there are always more tentacles than basal mesenteries. *Verrillactis paguri* (Verrill, 1869*a*) has more small mesenteries at the limbus than at the margin. It is possible for the mesenteries to appear normally at the margin and grow downwards, but further down the column to develop only into small elevations of tissue, seen in transverse section, to comprise mesogloea covered with endoderm (as in *Mesactinia ganensis* gen. nov., sp. nov., p. 263). Only careful observation, for example by bulk staining of the specimens, will detect their presence (p. 209).

The presence of just a few more mesenteries at margin or base is not considered to be of generic importance and such specimens can be classified under (b). Only when there are at least half a cycle more mesenteries present at margin or limbus should a specimen be referred to categories (a) or (c).

Nematocysts. The types and size-ranges of nematocysts have been used as taxonomic characters from species to family level. Carlgren (1949: 86) used the presence or absence of certain nematocyst types in the acontia to define families, and in many other papers he used their size-range to identify species. Hand (1955, 1956) was the first to illustrate all the cnidome of an individual species. He grouped them according to that part of the specimen from which the different types of nematocysts came (tentacles, column, actinopharynx, filaments and, when appropriate, nemathybomes, spherules and acontia). This method has been adopted here for the following reasons:

a. The diagrams show the shape and structure of the nematocysts found, and obviate confusion over the terms used to name them. Several names now exist for each nematocyst type. For example, a single type has been termed basitrich (Weill, 1934), microbasic b-mastigophore (Cutress, 1955: 128), b-rhabdoid (Schmidt, 1969: 298), and spirula (den Hartog, 1980: 7, after Stephenson, 1928: 62–63).

b. It provides a 'nematocyst signature' of each species which can be used for rapid comparison with the 'signatures' of others. When species belonging to different families and to some extent to different genera are compared, a clear distinction between 'signatures' is usually apparent. Figures 40–42 illustrate generic differences between three acontiate species. But when congeneric species are compared only small differences in the size ratios of the two or three nematocyst types in one part may separate species. Figures 19, 21, 23 and 25 illustrate the closeness of the 'signatures' in four congeneric species. In fact these 'signatures' are so similar that, in the absence of morphological information, they might have been interpreted as coming from a single species.

Taxonomic section

Suborder **NYNANTHEAE** Carlgren, 1898
Subtribe **ATHENARIA (ABASILARIA)** Carlgren, 1898
Family **EDWARDSIIDAE** Andres, 1881
Genus ***EDWARDSIA*** de Quatrefages, 1841

Edwardsia de Quatrefages, 1841: 427.
Scolanthus Gosse, 1853: 153.
Halcampa: Panceri, 1869: 1 (part).

NOMENCLATURE. An application to the International Commission on Zoological Nomenclature to conserve the generic name *Edwardsia* de Quatrefages, 1841, and the family name EDWARDSIIDAE Andres, 1881, was submitted by Williams (1979) and was favourably resolved in Opinion 1294 (*Bulletin of Zoological Nomenclature* 42: 31–33).

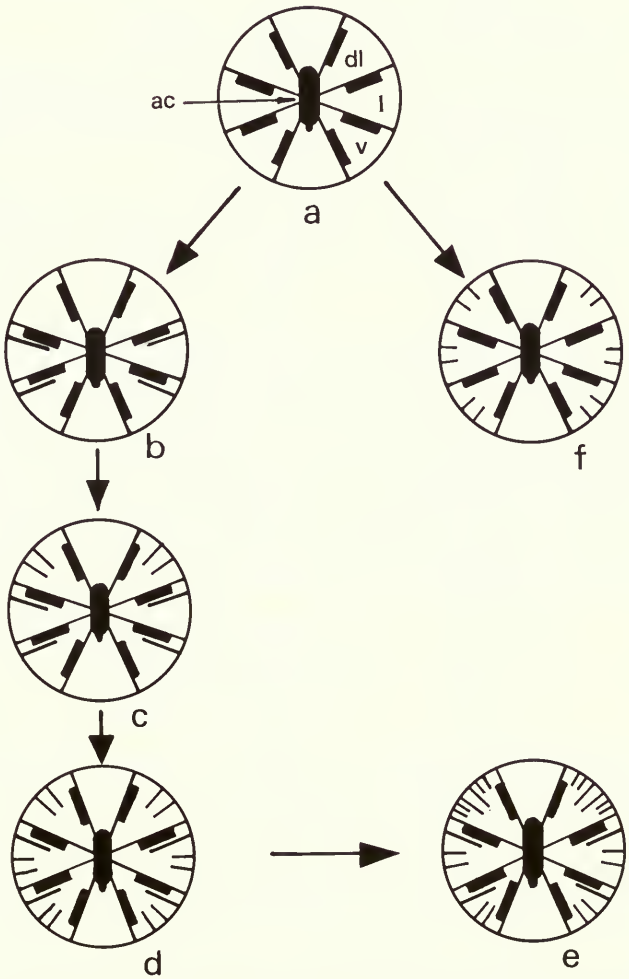

Fig. 4 *Edwardsia*. Development of mesenteries and their relation to the number of tentacles. (a) *'Edwardsia'* stage. (b) 12 tentacle stage. (c) 16 tentacle stage. (d) 24 tentacle stage. (e) 32 tentacle stage. (f) *'pudica'* arrangement, 20 tentacles. (ac actinopharynx, dl dorso-lateral exocoel, l lateral exocoel, v ventral exocoel. Retractor muscles represented as black rectangles; lumen of pharynx not shown.)

TYPE SPECIES. *Edwardsia beautempsi* de Quatrefages, 1842, by designation by Carlgren (1949: 23).

DEFINITION. Edwardsiidae (sensu Carlgren, 1949: 22) with column divided into physa, scapus, scapulus and capitulum; physa short, ampullaceous, without nemathybomes or cuticle. Scapus long with nemathybomes sunk in the mesogloea. *Nemathybomes always containing two types of nematocyst*. Siphonoglyph weak, ventral. Mesenteries comprising eight macrocnemes (perfect) and at least four microcnemes (imperfect) which are very weak and in capitulum only; *first four microcnemes always paired with macrocnemes*. Gonads, filaments, and parietal and retractor muscles on macrocnemes only. Parietal muscles well developed, retractors strong-diffuse to restricted-reniform. Cnidome: spirocysts, basitrichs, pterotrichs, microbasic amastigophores and t-mastigophores.

REMARKS. Fifty-five nominal species were referred to *Edwardsia* by Carlgren (1949) but only about four more have been described since, and some of the original fifty-five have been shown by Manuel (1977) and Williams (1981) to be invalid. Williams recognized 40 valid species, but much literature searching is still necessary before a single species can be confidently identified. The task can be reduced if certain species are eliminated on conspicuous taxonomic characters and placed in other genera. The two characters in question are the presence of one or two types of nematocyst in the nemathybomes, and the pattern of development of the microcnemes.

Carlgren (1921: 28) noticed that one type of nematocyst was present in the nemathybomes of some species of *Edwardsia* and two types in others. He used this character to differentiate between species, although he did not use it in his later survey of the whole order (Carlgren, 1949). Other authors have noted this character without using it taxonomically, though Williams (1981) listed the nominal species of *Edwardsia* under these and other headings.

In this work species with only one type of nematocyst (basitrichs) in the nemathybomes were separated from those with two types (pterotrichs and microbasic t-mastigophores, p. 219). The presence or absence of a type of nematocyst is usually considered to be of generic or higher significance.

The arrangement of the microcnemes is also regarded here as a generic character. Microcnemes develop after the eight macrocnemes in two ways. Normally four arise (Fig. 4a) in the lateral and ventral exocoels and are paired with the ventro-lateral and dorso-lateral couples, and four more arise as two pairs in each dorsal exocoel (Fig. 4b-c)). They correspond to the 16 tentacles. In some species the two pairs of microcnemes do not develop and there are only 12 tentacles instead of 16.

The plan of development may continue with four more pairs of microcnemes arising in the lateral and ventral exocoels, corresponding to 24 tentacles (Fig. 4d). In some species development continues with pairs of secondary microcnemes arising in the dorsal exocoels as well, one pair on each side of the first pair (Fig. 4e). Species with this arrangement have up to 32 tentacles.

Examples of species with each of these arrangements are:

12 tentacles	*E. duodecemtentaculata* Carlgren, 1931
16 tentacles	*E. longicornis* Carlgren, 1921
24 tentacles	*E. carneola* (Verrill, 1928)
32 tentacles	*E. timida* de Quatrefages, 1842

A maximum of 28 tentacles in *E. timida* was recorded by Manuel (1977: 492, Fig. 4), but his illustration shows that microcnemes were absent from the dorsal exocoels, only two pairs of microcnemes occurring there instead of the usual three pairs.

Up to 36 tentacles have been recorded in some species, for example *E. timida* (= *E. callianthus* Rawlinson, 1935) and *E. sipunculoides* (Stimpson, 1853; Carlgren, 1931). In such instances additional pairs of microcnemes occur in the lateral exocoels or, as shown by Stephenson (1935), in the ventral exocoels. Other anomalies are known. One microcneme of a pair may develop before the other resulting in an odd number of tentacles. This has been observed in *E. vivipara* Carlgren, 1950*c*. Dixon (1886) also noted anomalies, in *E. timida*.

The second pattern of development of microcnemes results in a quite different arrangement. After the eight macrocnemes have formed the four single microcnemes do not develop in the lateral and ventral exocoels but six pairs of microcnemes arise, one pair in each exocoel (Fig. 4f). This

results in 20 tentacles. It is not yet known whether all microcnemes appear at the same time, as seems probable, or whether they develop in certain exocoels first. This type of arrangement was first noted by Faurot (1895) in *E. adenensis* Faurot, 1895. Bourne (1916) drew attention to it when describing *E. rakaiyae* Bourne, 1916, and discussed a possible interpretation of the sequence of development of the tentacles and micromesenteries. Stephenson (1935: fig. 108A) found that same arrangement in an edwardsiid from Low Island on the Great Barrier Reef. The species was subsequently named *E. stephensoni* by Carlgren (1950*b*), but is here referred to *Edwardsianthus pudica* (Klunzinger, 1877) comb. nov. All recorded specimens of *E. pudica* have six pairs of microcnemes. Similarly, I have examined 57 specimens of *E. gilbertensis* (Carlgren, 1931) and all had six pairs. This arrangement of microcnemes separates the two species *E. pudica* and *E. gilbertensis* from those that develop mesenteries in the normal way.

Table 1 The species of *Edwardsia* de Quatrefrages, 1841.

Species	Number of Tentacles	Nemathybomes arrangement	Dimensions of nematocysts from nemathybomes (μm)	Source of data
E. annamensis Carlgren, 1943	16	rows	41·0–60·6 × 4·2–5·6 42·3–60·6 × 2·0–2·8	Carlgren, 1943: 19
[1]*E. beautempsi* de Quatrefages, 1842	16	rows	39·0–65·0 × 4·5–6·0 45·0–64·0 × 2·5–3·0	Manuel, 1977: 487
E. californica McMurrich, 1913	16	rows	115–153 × 6·3–7·0 72·0–77·0 × 2·5	Carlgren, 1936: 18
E. capensis Carlgren, 1938	18	rows	68.0–86.0 × 5.5–6·0 67·0–72·0 × 2·5	Carlgren, 1938: 19
E. claparedi (Panceri, 1869)	16	rows	97·0–154 × 5·0–7·0 69·0–95·0 × 2·5–3·0	Manuel, 1981: 198; 1977: 487
E. elegans Verrill, 1869*c*	16	rows	67·0–101 × 6·5–7·0 67·0–84·0 × 2·5–3.0	Carlgren, 1931: 16–18
E. hantuensis sp. nov.	16	rows	62·7–105·6 × 4·6–6·6 54·8–68·2 × 2·6	p. 222
[2]*E. ivelli* Manuel, 1975	16	rows	24·0–33·0 × 2·5–3·0 20·0–30·0 × 2·0–3·0	Manuel, 1975: 705–711
E. longicornis Carlgren, 1921	16	rows	36·0–84·0 × 3·5–5·0 36·0–65·0 × 2·0–2·5	Manuel, 1977: 487
E. maroccana Carlgren, 1931	16	rows	131–156 × 6·0 74·0–84·0 × 2·0–2·5	Carlgren, 1931: 15–16
E. octoradiata Carlgren, 1931	16	rows	55·0–79·0 × 3·5–4·0 35·0–43·0 × 2·5	Carlgren, 1931: 13–15
E. sanctaehelenae Carlgren, 1941	12	rows	56·4–81·8 × 5·0–5·6 42·3–49·3 × 2·0–2·5	Carlgren, 1941: 1
E. sulcata (Verrill, 1864)	14–16	rows	84·6–104·3 × 7·0 52·2–67·7 × 4·2	Carlgren, 1950*d*: 22
E. tintrix Annandale, 1915	16	rows	65·0–89·0 × 4.5 46·0–53·0 × 2·0–2·5	Carlgren, 1925: 19
E. tuberculata Düben & Koren, 1847	16	rows	(72)110–190 × 4·0–7·0 60·0–96·0 × 2·5	Carlgren, 1921: 29
E. carlgreni (Carlgren, 1921)	16	scattered	62·0–74·0 × 5·0 36·0–53·0 × 2·5	Carlgren, 1921: 3; see Williams, 1981: 351
E. danica Carlgren, 1921	14–20	scattered	46·0–72·0 × 4·5 24·0–43·0 × 2·0–3·5	Carlgren, 1921: 37
E. novazelanica Farquhar, 1898	16–24	scattered	41·0–56·0 × 3·5–4·5 34·0–41·0 × 2·0	Carlgren, 1924: 184–187 (*E. tricolor* Stuckey, 1908)
E. sipunculoides (Stimpson, 1853)	18–30	scattered	65·0–74·0 × 6·0 41·0–50·0 × 3·5	Carlgren, 1931: 22–23

[1]Type species of genus. [2]possibly *Edwardsioides*.

Using these two characters species whose nemathybomes have only basitrichs, that is, just one type of nematocyst, can be removed from the genus *Edwardsia* and subdivided into two new generic groupings based on the mesenterial arrangements. The species in which relevant data could be found in the literature are listed in Tables 1–3. The generic groupings are given in Figure 5.

Danielssen (1890) introduced the genus *Edwardsioides* to accommodate *E. vitrea* Danielssen, 1890. This is the earliest generic name available for the group comprising those species with only one nematocyst type in the nemathybomes and four microcnemes, paired with four macrocnemes.

The final group (Table 3) comprises those species with one type of nematocyst in the nemathybomes but no microcnemes in the first cycle of mesenteries. The generic name *Edwardsianthus* gen. nov. is proposed here with *Edwardsia pudica* Klunzinger, 1877, as the type species.

Further subdivision of the genera *Edwardsia, Edwardsioides* and *Edwardsianthus* is possible according to whether the nemathybomes are arranged in rows or scattered on the column. Subdivision is unnecessary in *Edwardsianthus* which has only two species and in *Edwardsioides* in which only one out of fourteen species has the nemathybomes arranged in rows. However, the 19 species referred to the genus *Edwardsia* can be divided with some advantage. They fall into two groups, 4

Table 2 The species of *Edwardsioides* Danielssen, 1890.

Species	Number of Tentacles	Nemathybome arrangement	Dimensions of nematocysts from nemathybomes (μm)	Source of data
E. andresi Danielssen, 1890	12	scattered	48·0–67·0 × 3·5–4·0	Carlgren, 1921: 49
E. arctica Carlgren, 1921	16	rows/ scattered	38·0–60·0 × 4·0–5·0	Nemathybomes scattered in proximal part. Carlgren, 1921: 39
E. duodecemtentaculata Carlgren, 1931	12	scattered	33·0–48·0 × 2·5–3·0	Carlgren, 1931: 4
E. finmarchica Carlgren, 1921	26	scattered	36·0–48·0 × 3·0–4·0	Carlgren, 1921: 55
E. fusca Danielssen, 1890	12	scattered	31·0–36·0 × 2·0–2·5	Carlgren, 1921: 28
E. islandica Carlgren, 1921	16	scattered	36·0–48·0 × 2·0–2·5	Carlgren, 1921: 47
E. japonica Carlgren, 1931	16	scattered	74·0–101 × 2·5–3·5	Carlgren, 1931: 12
E. kameruniensis Carlgren, 1927	20	scattered	45·0–63·0 × 3·5–4·5	Carlgren, 1927: 478
E. meridionalis Williams, 1981	16(18)	scattered	29·0–50·7 × 2·6–4·7	Williams, 1981: 325
E. norvegica Carlgren, 1942	16	scattered	47·0–58·0 × 3.0	Carlgren, 1942: 60
E. timida de Quatrefages, 1842	32	scattered	32·0–75·0 × 3·5–7·0	Manuel, 1977: 491
E. vegae Carlgren, 1921	16	scattered	84·0–100 × 3·0	Carlgren, 1921: 53
[1]*E. vitrea* Danielssen, 1890	16	scattered	36·0–42·0 × 3·0–3·5	Carlgren, 1921: 49
E. vivipara Carlgren, 1950*c*	16	scattered	26·8–38·1 × 3·5–4·5	Carlgren, 1950*c*: 1
E. jonesi Seshaiya & Cutress, 1969	12	rows	48·0–72·0 × 4·5–5·5	Seshaiya & Cutress, 1969: 73

[1]Type species of genus.

Table 3 The species of *Edwardsianthus* gen. nov.

Species	Number of Tentacles	Nemathybome arrangement	Dimensions of nematocysts from nemathybomes (μm)	Source of data
[1]*E. pudica* Klunzinger, 1877	20	scattered	37·0–44·0 × 2·5	Carlgren, 1931: 18–21 (see p. 227)
E. gilbertensis Carlgren, 1931	16–20	rows	31·0–41·0 × 2·0–3·0	Carlgren, 1931: 10–11

[1]Type species of genus.

species having the nemathybomes scattered on the column and 15 species having them in rows. This division has not been formalized here because it may be advantageous to subdivide the genus at a later date on a different character, namely the types of nematocyst in the nemathybomes (see p. 219).

Species of *Edwardsia* listed by Carlgren (1949: 23–24) and other authors but not included here have been omitted either because they have been shown to be conspecific with the species listed or because insufficient data is available to make it possible to place them in one of the three genera proposed. Williams (1981) listed all species referred to the genus *Edwardsia* with comments on their validity and synonyms.

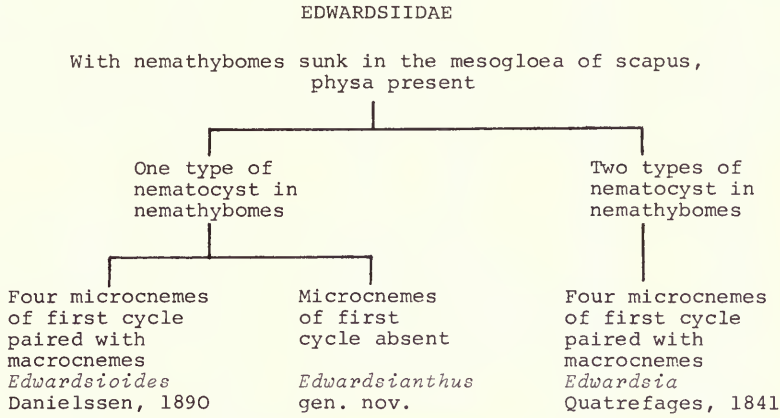

Fig. 5 Edwardsiidae. Distinctions between the genera *Edwardsia*, *Edwardsioides* and *Edwardsianthus* gen. nov.

Nematocyst types in the nemathybomes of Edwardsia. Manuel (1977: 488, Fig. 2) illustrated two types of nematocyst that he termed microbasic b-mastigophores from *E. beautempsi*, and two other types from *E. timida*. The types illustrated under *E. beautempsi* were not identical, but were similar to those described by Carlgren (1940*a*: 23, Fig. V, figs 7–8, 12–13) from *E. longicornis*. One type of nematocyst (Manuel 1977, Fig. 2E) differs from the normal b-mastigophore (or basitrich) in that the armature of the thread can be divided into four distinct regions. A similar nematocyst has been studied, both discharged and undischarged, from specimens referred to *E. tuberculata* Düben & Koren, 1847: 267, from off Rame Head, South Devon (Fig. 6a-c). The basal part of the thread is folded and bears a few short pointed spines arranged spirally, corresponding to Schmidt's 'faltstuck' (Schmidt 1969: 294, Fig. 5). Then follows a length of thread with a feature so far unique in nematocyst morphology (Fig. 6b). It is a heavily armed portion having many thick close-set spines that are not arranged spirally around the thread but lie in three rows along it. They recall in appearance the flight feathers of an arrow (Fig. 6b), rather than conforming to Carlgren's impression of a membrane. Above this extraordinary region there are a few large spines arranged spirally, reducing sharply in size to those of the longest and distalmost part of the thread which is armed with minute spines arranged spirally throughout its length. The basal part of the thread is no more than $1\frac{1}{2}$ times wider in diameter than the remainder. This nematocyst type, therefore, incorporates features of both haplonemes and mastigophores. Shaft and thread are of nearly the same diameter, resembling the basitrich in morphology, but a 'faltstuck' is present and the spines are set close together as in the mastigophore. The undischarged capsule resembles in appearance that of a basitrich, apart from the folded part of the thread near the tip of the capsule. The straight part of the thread, in the undischarged capsule, does not show evidence of the spines except at the bottom, but has a thin line running along its length in the centre. The bottom of the capsule contains most of the coiled part of the thread, only a small section of the thread extending into the upper part, as a loose loop (Fig. 6a). The armature of the coiled thread is clearly visible.

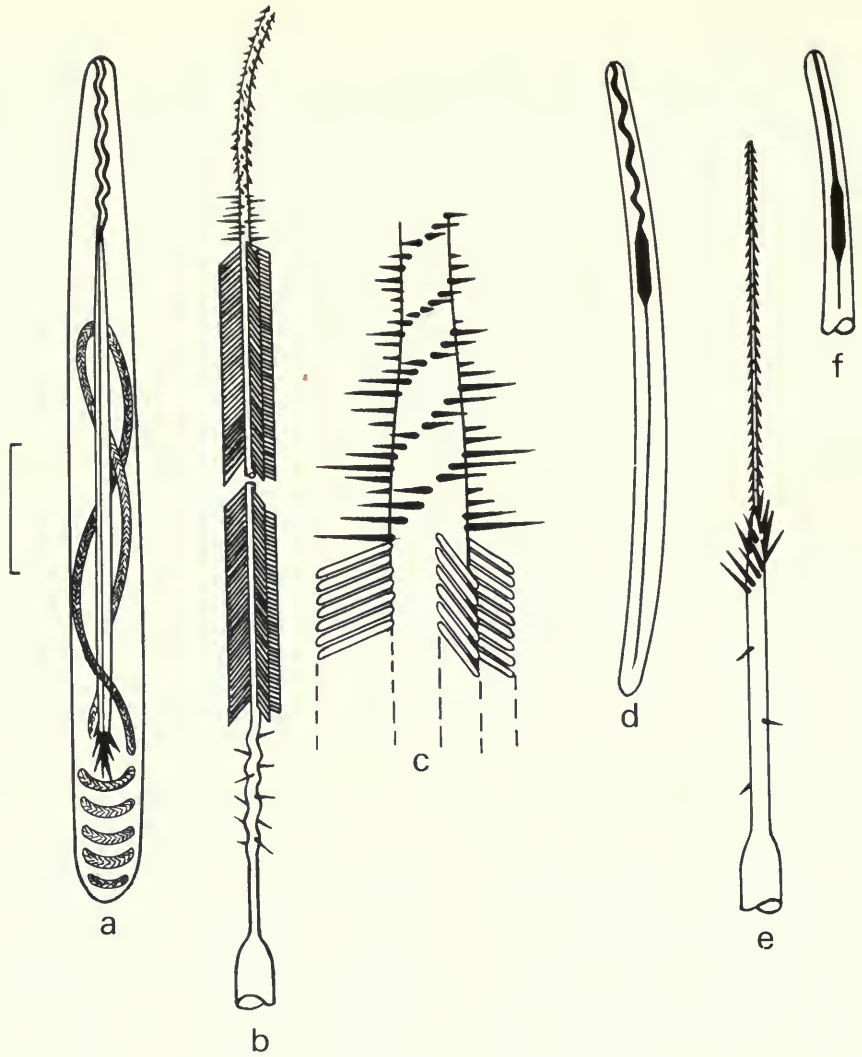

Fig. 6 Nematocysts of the nemathybomes of *Edwardsia tuberculata* (diagrammatic). (a) Undischarged pterotrich. (b) Discharged thread of same, showing types of spines and their arrangements on the thread. (c) Part of same enlarged. (d) Undischarged microbasic telotrichous mastigophore (t-mastigophore), with folded shaft. (e) Part of same, discharged, showing position of large spines at the head of the shaft. (f) Part of same showing alternative, unfolded shaft, undischarged. Scale: (a,d) = 20 μm, remainder not to scale.

Since the lower part of the thread is only slightly wider than the remainder, and because the undischarged capsule resembles a basitrich more than a mastigophore, I propose to classify this nematocyst type among the haplonemes. The name 'pterotrich' is suggested. The undischarged capsule can be recognised from the 'faltstuck' and the few large protruding spines at the end of the straight portion of the thread.

The other type of nematocyst (Carlgren 1940*a* Fig. V, figs 7–8; Manuel 1977, fig. 2F) is a mastigophore in that when discharged it shows a definite shaft with parallel sides and a distinct thread (Fig. 6d-f). The diameter of the shaft is some four times that of the thread, not with shaft and thread of the same diameter as illustrated by Carlgren. It cannot, however, be classified as a

b-mastigophore since the shaft has spines only at the forward end (Fig. 6e). Although the discharged capsule resembles Weill's (1934) microbasic euryteles there is no swelling at the end of the shaft and before discharge the capsule resembles rather a basitrich with a thickened portion in the centre of the straight part of the thread. Weill might possibly have termed this nematocyst a microbasic telotrichous mastigophore, for which the shortened form microbasic t-mastigophore is proposed.

Manuel (1977, figs 2G-H) illustrated two nematocysts of one type from the species *E. timida* which appear to be basitrichs, but from his illustrations it is not possible to be certain. If the two nematocysts are the same and two clearly defined size ranges are present then the nematocysts of this species differ from those of other *Edwardsia* species and a new genus would be appropriate to accommodate *E. timida*. Alternatively, if all nematocysts from the nemathybomes fall into a single range then the species might be transferred to the genus *Edwardsioides*. The figures quoted by Manuel (1977: 491) suggest that the species should be so referred. Other species currently included in *Edwardsia* (Table 2) may also present the same problem, the size-ranges of nematocysts overlapping in both length and diameter, for example *E. ivelli* Manuel, 1975: 705–711.

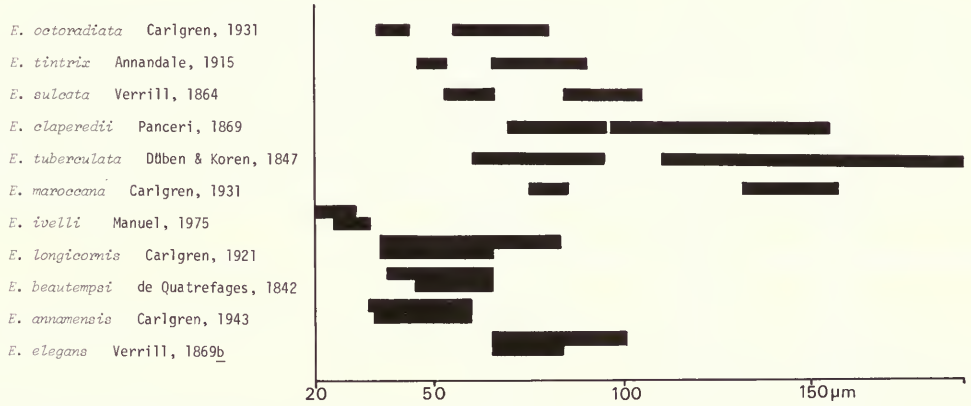

Fig. 7 Comparison of nematocyst size ranges in nemathybomes of certain edwardsiids. (Sources of data as in Table 1.)

A bar chart (Fig. 7) of the size ranges of nematocysts in the nemathybomes of species of *Edwardsia* shows an interesting variation. In certain species the two size ranges are distinct (*E. claparedi*, *E. tuberculata*), whereas in others the two ranges overlap (*E. beautempsi*, *E. longicornis*). These species are cited since the types of nematocyst in their nemathybomes are well known. It is too early to say if there is any significance in this variation, but it will at least assist in identifying species of *Edwardsia*.

Edwardsia hantuensis sp. nov.
Figs 8–9

MATERIAL EXAMINED. Singapore: Pulau Hantu, 1 specimen, 19 Sep 1970, BMNH 1983.4.8.1. Size in spirit 30 mm high, 5 mm wide.

DESCRIPTION. *External appearance.* Column divided into physa, scapus, scapulus and capitulum. Scapus with eight rows of large prominent nemathybomes and an easily removed cuticle. Near scapulus nemathybomes close together but towards physa further apart. Tentacles up to 16, long, smooth, tapered. *Anatomy.* Eight macrocnemes and up to eight microcnemes in typical *Edwardsia* manner. Retractors strong, diffuse, with 25–28 muscle processes, some branched, arising from mesogloeal sheet (Fig. 8a). Parietal muscles large, well developed, on both sides of mesogloea,

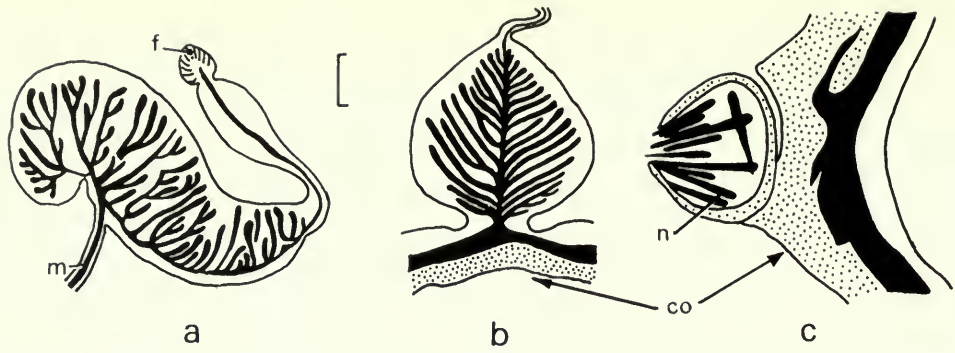

Fig. 8 *Edwardsia hantuensis* sp. nov. BMNH 1983.4.8.1. Transverse sections of (a) retractor muscle, (b) parietal muscle, (c) nemathybome. Scale: (a-c) = 50 μm. (co column, f filament, m mesentery, n nematocysts. Stippled, ectoderm; black, mesogloea; white, endoderm.)

cross-sectional area nearly half that of main retractor in same area of column (Fig. 8b). Microcnemes small. Nemathybomes (Fig. 8c) large, with both pterotrichs and microbasic t-mastigophores (p. 223, Fig. 9). Physa without a central pore but many cinclides present near tip of each exocoel. *Cnidome*. See Table 4 and Figure 9. The size ranges of the nematocysts of the nemathybomes are the overall ranges. The pterotrichs in the nemathybomes nearest the scapulus are smaller than those of the nemathybomes near the physa. For example, 62·7–75·8 × 4·0–5·3 μm near scapulus, 92·4–105·6 × 5·3–6·6 μm near physa. *Colour*. Column light sienna, nemathybomes white.

RECORDED DISTRIBUTION. Recorded only from Singapore (present material).

Table 4 Size ranges of cnidae of *Edwardsia hantuensis* sp. nov. compared with those reported from *E. sulcata* (Verrill) and *E. elegans* Verrill (in μm).

Location/ type of cnida	*E. hantuensis* sp. nov. Singapore (BMNH 1983.4.8.1)	*E. sulcata* (Verrill) Massachusetts from Carlgren, 1950*d*: 23	*E. elegans* Verrill Maine from Carlgren, 1931: 16
Tentacle			
Spirocyst	11·8–18·9 × 1·8–3·5	...	...
Basitrich	10·6–23·6 × 1·5	21·0–26·3 × 2·8–3·5	17(19)–29(31) × 2·5–3·0
Capitulum			
Basitrich	10·6–11·8 × 1·8	...	...
Nemathybome			
Pterotrich	62·7–105·6 × 4·6–6·6	84·6–104·3 × 7·0	67·0–101 × 6·5–7·0
Microbasic t-mastigophore	54·8–69·2 × 2·6	52·2–67·7 × 4·2	67·0–84·0 × 2·5–3·0
Actinopharynx			
Basitrich	11·8–26·0 × 2·0–3·5	...	12·0–16·0 × 1·5 29·0–36·0 × 2·5(3)
Microbasic amastigophore	26·0–30·7 × 5·8–7·0	...	29·0–31·0 × 5·0
Filament			
Basitrich	12·0–17·7 × 2·4	...	...
Basitrich	17·7–22·4 × 3·5	19·0–22·6 × 2·5–2·8(3·5)	...
Microbasic amastigophore	18·9–23·6 × 4·1–5·8	24·0–28·2 × 4·5–7·0	...
Microbasic p-mastigophore	21·2–28·3 × 3·5–4·1		

HABITAT. On reef flats in sand, Mean Low Tide Level (MLTL).

REMARKS. The presence of nemathybomes with both pterotrichs and microbasic t-mastigophores places this species in the genus *Edwardsia*.

The characters of this species are similar to those of *Edwardsia sulcata* (Verrill, 1864) sensu Carlgren, 1950*d*: 22, and *E. elegans* Verrill, 1869*c*. However, there are some differences in the

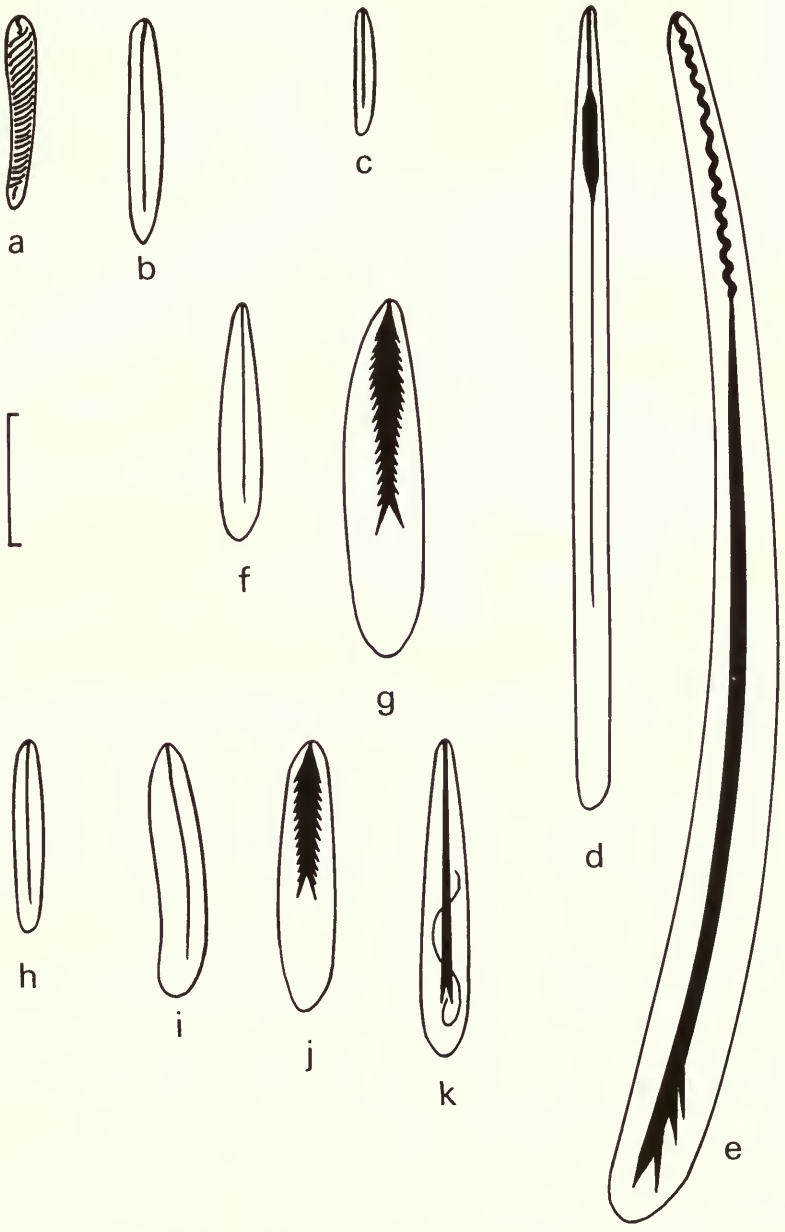

Fig. 9 *Edwardsia hantuensis* sp. nov., nematocyst signature (see Table 4). *Tentacle* (a) spirocyst, (b) basitrich. *Capitulum* (c) basitrich. *Nemathybome* (see Fig. 6) (d) microbasic t-mastigophore, (e) pterotrich. *Actinopharynx* (f) basitrich, (g) microbasic amastigophore. *Filament* (h-i) basitrichs, (j) microbasic amastigophore, (k) microbasic p-mastigophore. Scale: (a-k) = 10 μm.

nematocyst size ranges between these two species and the present material (see Table 4 for comparison). The large difference between the size ranges of the pterotrichs at top and bottom of the column may also be significant. Such differences have not been described before, as far as can be ascertained, and investigations into possible differences within specimens of other species are required.

The present material is, therefore, provisionally referred to a new species, *Edwardsia hantuensis* sp. nov.

Genus ***EDWARDSIOIDES*** Danielssen, 1890

Edwardsioides Danielssen, 1890: 100, pl. 5, fig. 3; pl. 16, figs 4–10.
Edwardsia: Carlgren, 1921: 28, 39, 43, 47, 53, 55; Carlgren, 1927: 478; Carlgren, 1931: 4–7, 12–13; Carlgren, 1942: 60; Carlgren, 1950*c*: 1; Seshaiya & Cutress, 1969: 73; Manuel, 1977: 491; Williams, 1981: 325.

DEFINITION. Body divisible into physa, scapus, scapulus and capitulum; physa short, without nemathybomes or cuticle. Scapus long with nemathybomes sunk in mesogloea and *containing only one type of nematocyst, basitrichs*. Siphonoglyph weak, ventral. Mesenteries: eight perfect (macrocnemes) and at least four imperfect (microcnemes) which are minute and usually confined to region of capitulum. *First four microcnemes always paired with macrocnemes*. Gonads, filaments, and parietal and retractor muscles on macrocnemes only. Parietal muscles well developed: retractors strong-diffuse to restricted-reniform. Cnidome: spirocysts, basitrichs, and microbasic amastigophores.

TYPE SPECIES. *Edwardsioides vitrea* Danielssen, 1890: 100, by present designation.

REMARKS. No specimen of this genus was found in the collection, but material of *E. vivipara* Carlgren (1950*c*: 1–2, fig. 1) from South Australia has been examined and the type of nematocyst in the nemathybomes in that species confirmed as a basitrich.

Genus ***EDWARDSIANTHUS*** nov.

Edwardsia: Klunzinger, 1877: 80; Faurot, 1895: 121; Carlgren, 1900: 46; Bourne, 1916: 517–518; Carlgren, 1931: 7; Carlgren, 1950*b*: 428, (part).
Edwardsiella Andres, 1883: 305 (part).

DEFINITION. Body divisible into physa, scapus, scapulus and capitulum; physa short, without nemathybomes or cuticle. Scapus long with nemathybomes sunk in mesogloea; cuticle present. Nemathybomes having only one type of nematocyst, basitrichs. Tentacles usually 20. Siphonoglyph weak, ventral. Eight perfect mesenteries (macrocnemes) and six pairs of imperfect mesenteries (microcnemes), minute and restricted to distal part of column. Imperfect mesenteries never paired with perfect mesenteries. Gonads, filaments, and parietal and retractor muscles on macrocnemes only. Parietals well developed; retractors strong-diffuse to restricted-reniform. Cnidome: spirocysts, basitrichs, microbasic amastigophores.

TYPE SPECIES. *Edwardsia pudica* Klunzinger, 1877, by original designation.

Edwardsianthus pudica (Klunzinger, 1877) comb. nov.
Figs 10–12

Edwardsia pudica Klunzinger, 1877: 80, pl. 6, fig. 3; Carlgren, 1931: 18–20, figs 16–17.
Edwardsiella pudica Andres, 1883: 309; Carlgren, 1900: 46, pl. 1, fig. 5.
Edwardsia adenensis Faurot, 1895: 121, pl. 6, fig. 5, pl. 7, fig. 6, text-figs 8–9.
?Edwardsia vermiformis Bourne, 1916: 517, pl. 51, fig. 3.
Edwardsia rakaiyae Bourne, 1916: 518, pl. 51, fig. 4, text-fig. 1.
Edwardsia bocki Carlgren, 1931: 7–9, figs 5–6.
Edwardsia stephensoni Carlgren, 1950*b*: 428–429, figs 1–2.

MATERIAL EXAMINED. Singapore: Pulau Jong, 1 specimen, 17 May 1970, BMNH 1983.4.8.2; Pulau Hantu, 2 specimens, 19 Sep 1970, BMNH 1983.4.8.3–4; Pasir Panjang, 1 specimen, 23 Feb 1971, BMNH 1983.4.8.5. Aden: below Jebel Hadid, 5 specimens, Aug 1966, BMNH 1983.4.8.6–9.

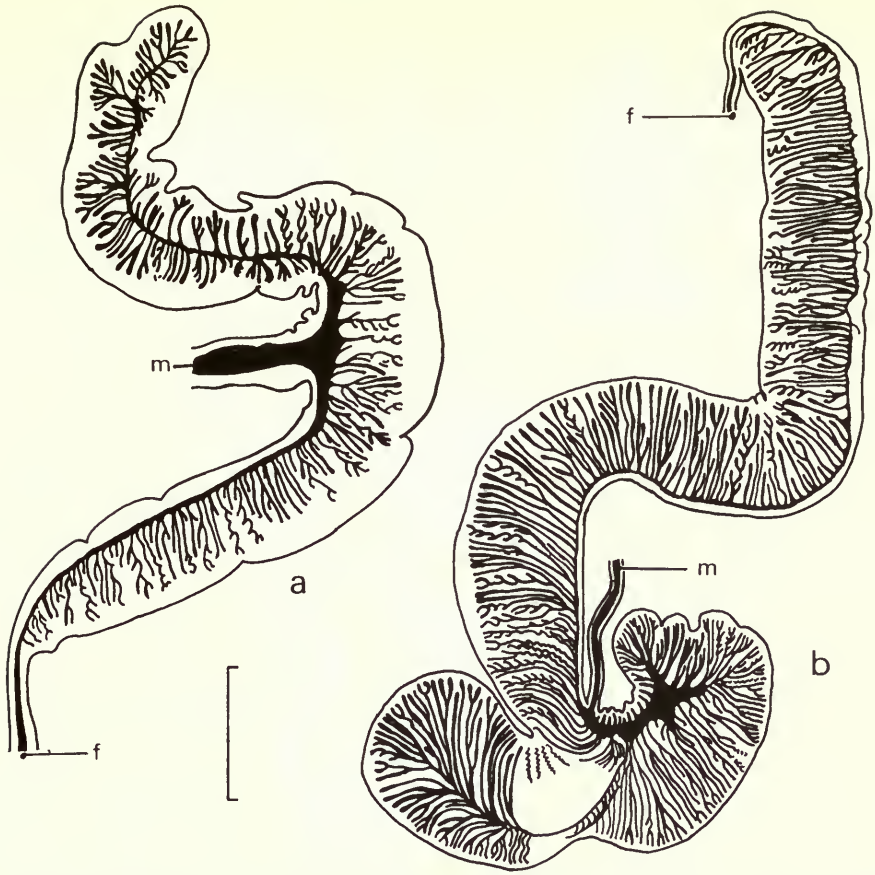

Fig. 10 *Edwardsianthus pudica* comb. nov. Variation in size and development of retractor muscles seen in transverse sections of two specimens: (a) Aden, BMNH 1983.4.8.6; (b) Singapore, BMNH 1983.4.8.3. Scale: (a-b) = 500 μm. (f filament, m mesentery, black, mesogloea; white, endoderm.)

Madagascar, 3 part specimens, Thomassin coll., Museum National d'Histoire Naturelle, Paris. Great Barrier Reef: *Edwardsia stephensoni* (syntypes), 3 specimens, BMNH 1954.6.28.3–4,6. In addition a specimen was seen alive on Gan Island, Addu Atoll, Maldives, March 1970, but not collected.

Description. Height up to 200 mm, diameter up to 15 mm. Divisions of column distinct. Capitulum thin walled, translucent, mesenteries within clearly visible in life; scapulus thin walled, lacking nemathybomes and cuticle, scapus thick walled, cuticle easily removed, with numerous small nemathybomes scattered irregularly over its length becoming most numerous towards physa, physa thin walled, lacking nemathybomes or terminal pore but having cinclides which are mostly endodermal evaginations; ectodermal suckers or tenaculi occasionally present (Fig. 11c). Tentacles up to 20, in two cycles 8, 12; long, slender, tapered. Mouth raised on cone. *Anatomy*. Eight macrocnemes arranged according to *Edwardsia* plan, one pair of microcnemes in each of the six exocoels. Microcnemes extremely small; having appearance of a pair of lips. In sections musculature comprising a single vertical layer of fibres over the complete surface. Microcnemes not extending below capitulum. Macrocnemes with both retractor muscles and parietal muscles well developed (Figs 10a-b, 11a-b); in sections retractors (Figs 10a-b) diffuse, with numerous closely packed high muscle folds, branched and unbranched, sometimes arranged in a pattern of several unbranched folds together, followed by one or sometimes 2-3 branched folds with a series

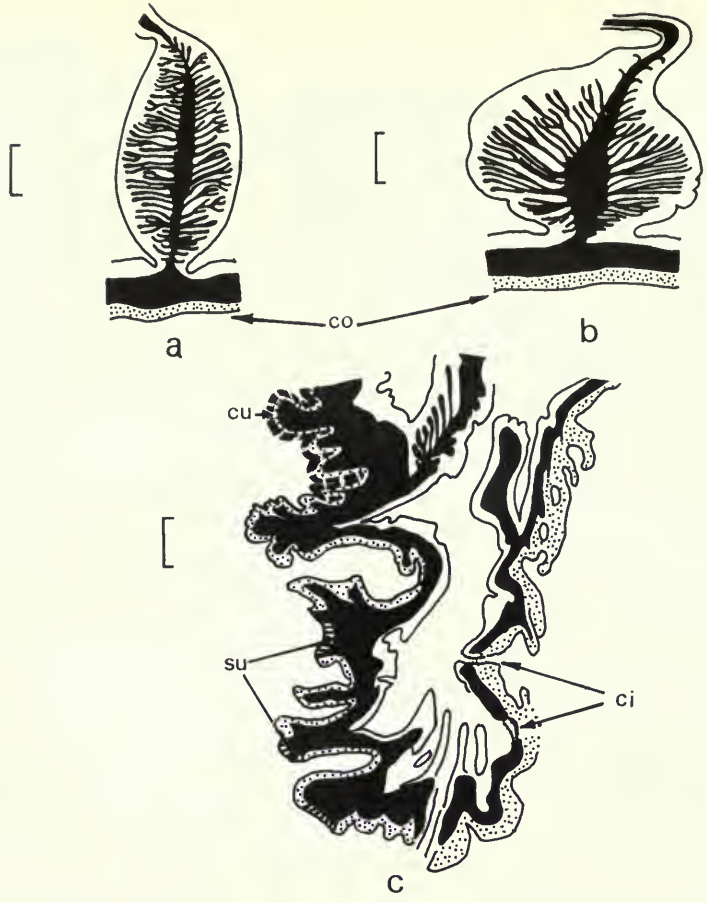

Fig. 11 *Edwardsianthus pudica* comb. nov. (a) Transverse section of parietal muscle, Aden, BMNH 1983.4.8.6; (b) Transverse section of parietal muscle, Singapore, BMNH 1983.4.8.3; (c) Vertical section through physa, Aden, BMNH 1983.4.8.6. Scale: (a-b) = 100 μm, (c) = 250 μm. (ci cinclides, co column, cu cuticle, su suckers. Barred, cuticle; stippled, ectoderm (modified at suckers); black, mesogloea; white, endoderm.)

of small curved off-shoots. Near column wall retractor is circumscribed, that is developing on both sides of extended mesogloeal sheet (Figs 10a,b). This part of mesogloeal sheet continuous with that of mesentery and sometimes itself branched (Fig. 10b). Parietal muscles well developed equally on each side of mesentery (Fig. 11a-b). Macrocnemes fertile, species apparently dioecious. Longitudinal muscles of tentacles ectodermal with short unbranched folds. Zooxanthellae present in endoderm of disk, tentacles, capitulum and actinopharynx. *Cnidome*. See Table 5 and Figure 12. *Colour*. Column light sienna, nemathybomes white. Capitulum delicate translucent purple to white. Tentacles of two colour varieties (a) delicate magenta-pink with thin purple line running from white tip to disk, (b) light-green with thin orange line. Disk white to cream.

Distribution. Recorded from the Red Sea (Klunzinger, 1877), Aden (Faurot, 1895, as *E. adenensis*, and present material), Zanzibar (Carlgren, 1931), the Maldives, Singapore (present material), Papua New Guinea (Bourne, 1916 as *E. rakaiyae* and possibly as *E. vermiformis*), Fidschi Island (Carlgren, 1931 as *E. bocki*) and the Great Barrier Reef (Carlgren, 1950*b*, as *E. stephensoni*).

Habitat. MLTL on reef flats or shores, in coarse or muddy sand.

Table 5 Size-ranges of cnidae of *Edwardsianthus pudica* comb. nov. (in μm).

Location/ Type of cnida	Localities of specimens				
	Singapore (BMNH 1983.4.8.3)	Singapore (BMNH 1983.4.8.4)	Aden (BMNH 1983.4.8.7)	Aden (BMNH 1983.4.8.9)	*E. stephensoni* Low Isle (BMNH 1954.6.28.3)
Tentacle					
Spirocyst	9·4–18·9 × 1·7–3·0	10·6–17·1 × 1·7–3·5	11·8–20·0 × 1·7–3·6	11·8–21·2 × 1·7–3·0	13·3–23·8 × 2·6–3·0
Basitrich	14·2–29·5 × 2·5–3·0	8·2–27·1 × 1·7–2·4	14·2–23·6 × 1·7–2·4	11·8–27·1 × 2·4	14·0–29·6 × 2·2–3·5
Capitulum					
Basitrichs	...	10·6–11·8 × 1·7	...	10·6–13·0 × 2·4	12·0–17·9 × 2·6
Nemathybome					
Basitrich	41·3–52·0 × 3·0	35·4–41·3 × 3·0–3·5	42·5–49.6 × 2·4–3·0	44·8–55·4 × 2·5–3·0	36·0–46·5 × 2·8–3·0
Actinopharynx					
Basitrich	17·7–43·7 × 2·5–3·5	11·8–30·7 × 1·7–3·0	17·7–28·3 × 1·7–3·5	14·2–33·0 × 4·1–5·3	11·3–33·0 × 2·6–3·3
Microbasic amastigophore	31·9–37·8 × 5·8–7·0	20·1–30·7 × 4·7	29·5–30·7 × 5·8–8·2	28·3–33·7 × 4·1–5·3	23·2–29·8 × 4·0–4·6
Filament					
Basitrich	13·0–33·0 × 1·7–3·0	11·8–33·0 × 2·5–3·0	11·8–27·1 × 1·7–3·5	16·5–31·8 × 1·7–3·0	12·7–31·7 × 2·8–3·3
Basitrich	31·0–40·1 × 4·7–5·8	27·1–35·4 × 2·5–3·0	21·2–30·7 × 3·0–4·1	27·1–33·0 × 3·0–3·5	30·4–39·0 × 3·5–4·5
Microbasic amastigophore	26·0–31·9 × 5·8–7·0	22·4–27·1 × 5·2–5·8	18·9–24·8 × 4·7–5·8	22·4–28·3 × 4·1–4·7	22·6–32·4 × 4·2–6·0

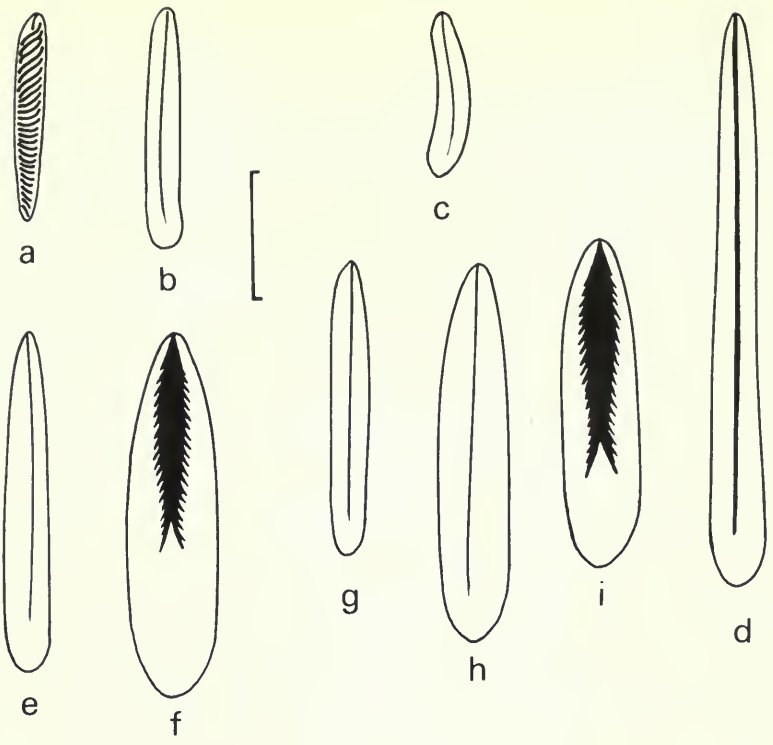

Fig. 12 *Edwardsianthus pudica* comb. nov., nematocyst signature (see Table 5). *Tentacle* (a) spirocyst, (b) basitrich. *Capitulum* (c) basitrich. *Nemathybome* (d) basitrich. *Actinopharynx* (e) basitrich, (f) microbasic amastigophore. *Filament* (g-h) basitrichs, (i) microbasic amastigophore. Scale: (a-i) = 10 μm.

Remarks. Five specimens from Aden resembled *Edwardsia pudica* Klunzinger, 1877, and *sensu* Carlgren (1900, 1931). That is, they had scattered small nemathybomes over the whole scapus containing only one type of nematocyst, and also 20 tentacles, corresponding to eight macrocnemes and six pairs of microcnemes, an arrangement unique in this genus. The three Singapore specimens were smaller and more delicate than those from Aden, but they had better developed retractor muscles in that the free edge of the retractor had a branched fold: however, this is a difference in degree (Fig. 10b). No other differences were found and since the other characters were similar, the specimens were referred to the present species.

The mesenterial arrangement is unusual in that it does not follow the usual development to the simple *Edwardsia* stage (p. 215). Other nominal species having this arrangement are *E. gilbertensis* Carlgren, 1931, *E. stephensoni* Carlgren, 1950*b* and *E. bocki* Carlgren, 1931. *E. gilbertensis* would seem valid since its nemathybomes are arranged in eight rows and the retractors poorly developed in contrast to the arrangements in *E. pudica*. The descriptions of both *E. stephensoni* and *E. bocki* closely resemble that of *E. pudica* suggesting that the three are conspecific. In the first two of these nominal species the retractors of the macrocnemes as illustrated by Carlgren are strong and well developed and the individual muscle folds follow the same plan as in *E. pudica*. That is, there are several unbranched folds followed by one or more branched folds, the pattern repeating itself along the muscle. The nemathybomes in both species are small, and scattered over the scapus. Also, the nematocysts are of the same type and have the same size range as in *E. pudica*. Carlgren did not record the presence of microbasic amastigophores in the actinopharynx, though they were scarce. The only description of *E. bocki* was made before nematocysts had been classified. *E. stephensoni* is conspecific with *E. pudica* and so apparently is *E. bocki*.

Two of the five nominal species described by Bourne (1916) from Papua New Guinea appear similar to *E. pudica*. These are *E. vermiformis* and *E. rakaiyae*. Bourne stated: '*E. vermiformis* . . . the muscle banners which were evidently large, with complicated, much branched folds . . . characteristic edwardsian structures (nemathybomes) are scattered over the areas between the longitudinal grooves of the scapus'. '*E. rakaiyae* . . . micromesenteries . . . 12 in number, two each sulco-lateral, lateral, or sulculo-lateral inter-mesenterial spaces'. Although Bourne's illustrations are inadequate for identification, his descriptions clearly include characters of *E. pudica*. Bourne himself suggested that *E. vermiformis* was similar to Klunzinger's figure, but without looking at the tentacles, disk and actinopharynx of the specimen it would be difficult to be certain. The well developed retractor muscle of *E. pudica* is the largest known of any *Edwardsia* species. Therefore, the presence of much branded mesogloeal folds of the retractors and the nemathybomes scattered over the column indicate that *E. vermiformis* might be referred to *E. pudica*.

From the details given by Bourne of *E. rakaiyae* there is little doubt that the species is identical with *E. pudica*. The presence of pairs of microcnemes between the main mesenteries, the 20 tentacles arranged 8+12, the enormously developed retractors, and the nemathybomes scattered over the column, are all diagnostic. Hence *E. rakaiyae* is referred to *E. pudica*.

A search for Bourne's material was made by R.L. Manuel at Oxford University but only one of his original slides, of *E. mamillata*, was found. *E. mamillata* seems not closely related to *E. pudica* since the retractor muscle is very weak. If the material were found it might still be possible to identify the species from the nematocysts in the nemathybomes and the arrangement of mesenteries.

Genus ***SCOLANTHUS*** Gosse, 1853.

Scolanthus Gosse, 1853: 157; Manuel, 1981: 266.
Edwardsia: Gosse, 1860: 254; Fischer, 1888: 22; Carlgren, 1931: 2.
Isoedwardsia Carlgren, 1921: 56; Carlgren, 1949: 24.
Alfredus Schmidt, 1979: 212.

Definition. Edwardsiidae with column divided into capitulum, scapulus and scapus. Proximal part of body rounded and like rest of scapus with nemathybomes scattered or in rows. Scapus with more or less well developed cuticle. Tentacles 16—20. Siphonoglyph ventral, feebly developed. Mesenteries, retractors and parietal muscles as in *Edwardsia*. Ciliated tracts of filament sometimes discontinuous. Cnidome: spirocysts and basitrichs; possibly also microbasic amastigophores in one species.

Type Species. *Scolanthus callimorphus* Gosse, 1853: 159, by monotypy.

Remarks. Manuel (1981) suggested that species having microbasic amastigophores and once referred to the genus *Isoedwardsia*, itself referred to *Scolanthus*, should be placed in a separate genus. The presence or absence of a type of nematocyst is usually considered to be a character of generic or higher importance. Certainly *S. armatus* (see below) does not have microbasic amastigophores and, from published data on the six species of *Isoedwardsia* originally included, only *I. nidarosiensis* Carlgren, 1942: 61, has this type of nematocyst. The descriptions of the other species were published between 1920 and 1931 at a time when Carlgren and other workers did not differentiate between types of nematocysts. *I. nidarosiensis* is provisionally referred to *Scolanthus* until the type specimen can be re-examined.

Scolanthus armatus (Carlgren, 1931) comb. nov.
Figs 13–14

Edwardsia armata Carlgren, 1931: 2–4, figs 1–2; Carlgren, 1949: 24.

Material Examined. Singapore: Pulau Hantu, 2 specimens, 19 Sept 1970; Pasir Panjang and Pungol Point, 1 specimen each location, 11 Feb 1971, BMNH 1983.4.8.10–13. Great Barrier Reef: Three Isles, 1 specimen, University of Queensland Expedition, 1973.

Description. Column divided into capitulum, scapulus and scapus. Proximal end of scapus

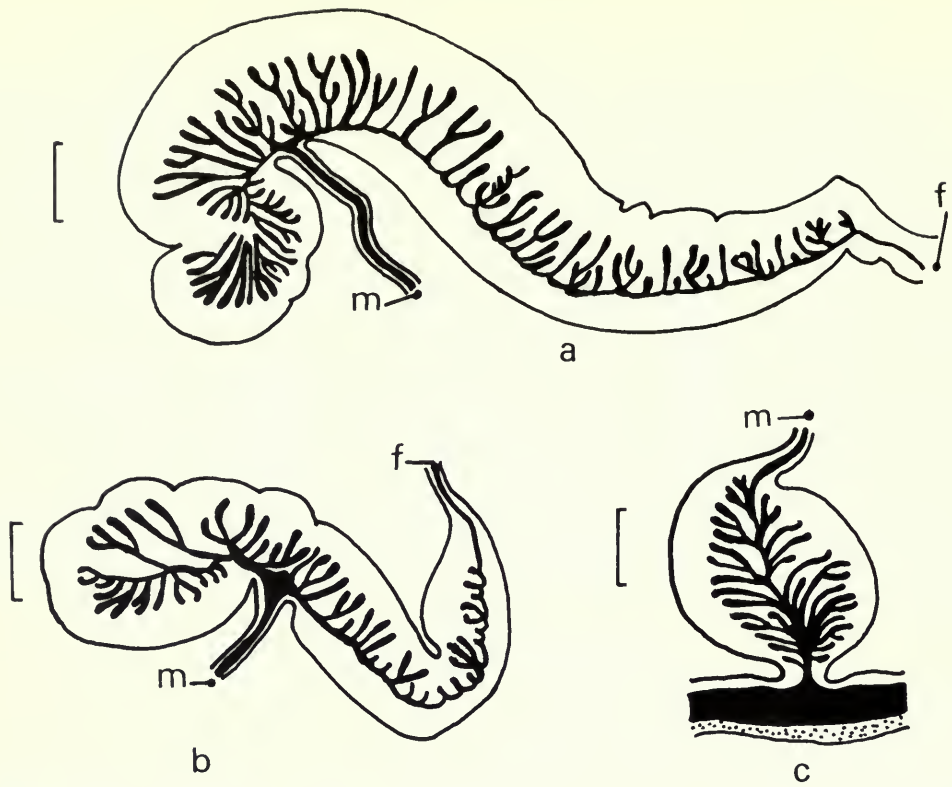

Fig. 13 *Scolanthus armatus* comb. nov. (a-b) Transverse section of retractor muscles, BMNH 1983.4.8.10–11. (c) Same specimen as (a), transverse section of parietal muscle. Scale: (a) = 100 μm, (b) = 20 μm, (c) = 40 μm. (m mesentery, f filament, Stippled, ectoderm; black, mesogloea; white, endoderm.)

Table 6 Size ranges of cnidae of *Scolanthus armatus* comb. nov. (in μm).

	Localities of specimens			
Location/ Type of cnida	Singapore (BMNH 1983.4.8.10)	Singapore (BMNH 1983.4.8.11)	Singapore (BMNH 1983.4.8.13)	Fiji *Edwardsia armata* (after Carlgren 1931: 2)
Tentacle				
Spirocyst	18·8–27·1 × 1·2–1·8	13·0–23·6 × 1·8	13·0–24·8 × 1·8–2·4	19·0–26·0 × 2·0–2·5
Basitrich	47·2–87·3 × 3·0–4·1	42·5–81·4 × 3·0–4·1	47·2–70·8 × 4·1–4·7	52·0–72·0 × 3·0–3·5
Capitulum				
Basitrich	11·8–15·3 × 2·4	...	...	...
Nemathybome				
Basitrich	43·7–76·6 × 4·1–5·8	47·2–70·8 × 4·1–5·8	63·7–69·6 × 4·1	40·0–70·0 × 3·5–4·5
Actinopharynx				
Basitrich	24·8–31·9 × 2·4	21·2–28·3 × 2·4–3·0	28·3–30·7 × 2·4	17·0–24·0 × 2·0–2·5
Basitrich	43·7–64·9 × 2·4–4·7	43·7–51·9 × 4·1–4·7	38·9–47·2 × 4·7–5·8	34·0–41·0 × 4·5–5·0
Filament				
Basitrich	23·6–33·0 × 2·4–3·0	22·4–29·5 × 3·0	27·0–36·5 × 2·4–3·0	...
Basitrich	39·0–48·3 × 3·5–4·7	25·0–47·2 × 3·5–4·7	33·0–49·6 × 4·7–5·8	...

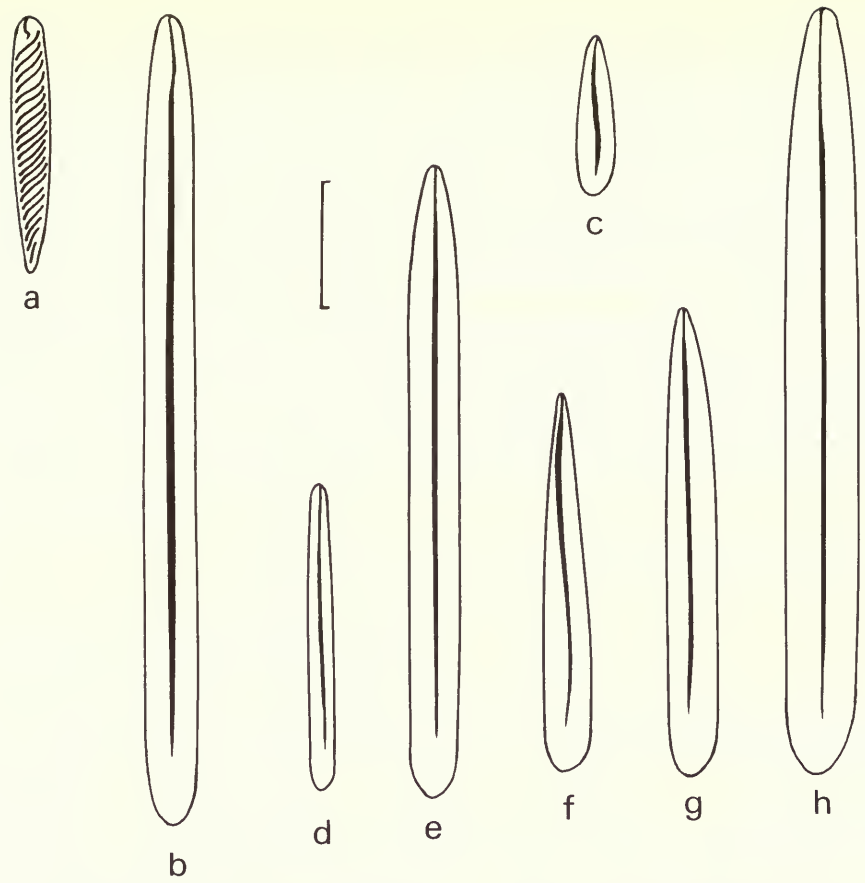

Fig. 14 *Scolanthus armatus* comb. nov., nematocyst signature (see Table 6). *Tentacle* (a) spirocyst, (b) basitrich. *Capitulum* (c) basitrich. *Actinopharynx* (e-f) basitrichs. *Filament* (g-h) basitrichs. Scale: (a-h) = 10 μm.

normally rounded but may be flattened by attachment to stones. Scapus with small, prominent, but irregularly scattered nemathybomes extending to proximal tip of column. Scapulus indistinct, without nemathybomes. Capitulum distinct, mesenterial insertions into endoderm visible through transparent wall. Tentacles up to 16, long, slender, capitate. Mouth at top of cone. Column in preserved specimens 45 mm high, 5 mm wide. *Anatomy*. Eight macrocnemes and up to eight microcnemes, developing in normal *Edwardsia* pattern. Microcnemes of dorsal exocoels developing last, normally in pairs but both of a pair not always arising together. Retractors of macrocnemes strong, diffuse (Fig. 13a-b), outer part developing as extension of mesentery whence muscle folds arise on both sides of mesogloeal sheet. Microcnemes small, confined to region of capitulum. Parietal muscles well developed. *Cnidome*. See Table 6 and Figure 14. *Colour*. Capitulum translucent with red markings, scapus light orange-brown with white nemathybomes. Tentacles translucent with white capitate tips.

Distribution. Fidschi Island, Viti Levu, Fiji (Carlgren, 1931). Singapore: Pulau Hantu, Pasir Panjang and Pungol Point; Great Barrier Reef: Three Isles (present material).

Habitat. In coarse to muddy sand, MLTL. Often with other edwardsiid species, for example *Edwardsia hantuensis* sp. nov., *Edwardsianthus pudica* comb. nov. and *Edwardsianthus gilbertensis* comb. nov.

REMARKS. The present material resembles *Edwardsia armata* Carlgren, 1931, in having irregularly scattered nemathybomes, 16 tentacles with prominent capitate tips bearing large nematocysts, and an identical mesenterial arrangement. The size range and types of cnidae given by Carlgren also correspond although in the actinopharynx the nematocysts of the present material were larger than in that studied by him. However, the size range of cnidae can vary a little within any species (Table 6) and the range may be usual in this species. Carlgren assumed that the rounded lower end of the column of this species was a physa, an assumption easily made when the cuticle is missing. However, sections of the present material revealed no physa. The nemathybomes and cuticle, reduced in thickness, were present almost to the base of the proximal end. Such specimens cannot be referred to the genus *Edwardsia* and should be placed in the genus *Scolanthus* (= *Isoedwardsia*) (see Manuel 1981).

There seems to be no other species referred to the genera *Isoedwardsia* and *Scolanthus* which these specimens resemble. None has capitate tips, and the cnidae are different in size (Table 7). The present specimens are, therefore, referred to *S. armatus*.

I am grateful to Mrs U. Canfield for drawing my attention to the absence of a physa in this species.

Table 7 The species of *Scolanthus*.

Species	Number of Tentacles	Nemathybome arrangement	Dimensions of nematocysts from nemathybomes (μm)	Source of data
S. armatus (Carlgren, 1931)	16	scattered	43·7–76·6 × 4·1–5·8	p. 230
[1]*S. callimorphus* Gosse, 1853	16	scattered	60·0–90·0 × 3·0–5·0	Manuel, 1981: 265
S. curacaoensis Pax, 1924	16	scattered	38(43)–53 × 2·5(3)	Carlgren, 1931: 26
S. ignotus (Carlgren, 1920)	17–20	scattered	34·0–48·0 × 3·0–3·5	Carlgren, 1920: 149
S. ingolfi (Carlgren, 1921)	16	scattered	50·0–60·0 × 4·0–5·0	Carlgren, 1921: 56
? *S. nidarosiensis* (Carlgren, 1942)	16	scattered	62·0–67·0 × 2·5–3·0	Carlgren, 1942: 61

[1]Type species of genus.

Tribe **THENARIA** Carlgren, 1898
Family **ALICIIDAE** (Duerden, 1895; Duerden, 1897)
Genus ***TRIACTIS*** Klunzinger, 1877

Triactis Klunzinger, 1877: 85; Carlgren, 1949: 44; Carlgren, 1950*b*: 433.
Viatrix: Haddon & Shackleton, 1893: 127 (part).
Hoplophoria Haddon, 1898: 438 (part).
Phyllodiscus: Stephenson, 1922: 280 (part); Carlgren, 1940*a*: 31.

DEFINITION. (*sensu* Carlgren, 1949: 44). Aliciidae with well developed pedal disk. Column divided into capitulum and scapus, sometimes scapus with small vesicles below margin. *Margin with stalked outgrowths (peduncles)* which in young specimens occur sparingly and are little branched, in older ones close together and dichotomously branched. Hemispherical mastigophoral spherules on stalks near branches of peduncles *and in fosse*. Stalks few, with longitudinal weak bands of endodermal muscle. Sphincter weak or absent. Tentacles hexamerously arranged, distally with spots as on column. Longitudinal muscles of tentacles and muscles of oral disk ectodermal. Two siphonoglyphs. Six pairs of perfect mesenteries and several imperfect pairs. Two pairs of directives. Retractor and parietobasilar muscles weak. Cnidome: spirocysts, basitrichs, microbasic and macrobasic amastigophores, possibly also microbasic b-mastigophores.

TYPE SPECIES. *Triactis producta* Klunzinger, 1877, by monotypy.

REMARKS. Carlgren (1949: 44) stated that the outgrowths of the column occurred in the middle, but later he stated that 'the upper part of the column (the capitulum) above the outgrowths is more thin walled than the lower part, and somewhat narrower just above them, and has ectodermal muscles and groups of spirocysts' (Carlgren, 1950*b*: 433). Two comments on Carlgren's views can be made. Firstly, the peduncles are outgrowths of the margin and not of the middle of the column, so that Carlgren's later statement is correct. The difference in thickness between the column wall and the capitulum is shown in Figure 15. Secondly, the presence of spirocysts in the capitulum was not confirmed. Examination of serial sections from two specimens did not reveal any spirocysts in this region and they occurred only in the tentacle tips. The nematocysts of the capitulum are microbasic amastigophores and basitrichs (microbasic b-mastigophores?). However, the presence of weak ectodermal muscle in the capitulum is confirmed.

The generic definition of *Triactis* is modified from that given by Carlgren (1949) to reflect the position of the peduncles and the presence of a capitulum. His reference to vesicles on the pedicels and peduncles is amended to spherules (see p. 210). Carlgren (1949) specified no sphincter but in one of the present specimens a weak sphincter was apparent, recalling that depicted by Haddon (1898: 439, text fig.) in *Hoplophoria cincta*. However, this may have been due to the influence of other muscles on the degree of folding of the circular muscles of the column. In a second specimen no sphincter was found.

Triactis producta Klunzinger, 1877
Figs 15–16

Triactis producta Klunzinger, 1877: 85, p. 6, fig. 8.
Viatrix cincta Haddon & Shackleton, 1893: 127.
Hoplophoria cincta Haddon, 1898: 438–439, pl. 23, figs 11–15.
Phyllodiscus indicus Stephenson, 1921: 561, fig. 18; Stephenson, 1922: 280; Stephenson, 1928: 18, fig. 11.
Phyllodiscus cinctus Stephenson, 1922: 280; Stephenson, Stephenson & Tandy, 1931: 38; Carlgren, 1940*a*: 31, fig. 8.2.
Triactis cincta: Carlgren, 1945: 7; Carlgren, 1947: 14; Carlgren, 1950*b*: 433.

MATERIAL EXAMINED. Aden: 14 specimens, 17 Jul 1966, BMNH 1983.4.8.27–30. Singapore: Pulau Semakau, 42 specimens, 22 Feb 1970, BMNH 1983.4.8.14–24; Pulau Biola, 2 specimens, 13 Sept 1970, BMNH 1983.4.8.25–26.

DESCRIPTION. Column with scapus and capitulum, definite margin, and deep fosse. Margin with peduncles each branched into several pedicels, the latter each terminating in or capped by a small mastigophoral spherule. Large mastigophoral spherules on upper surfaces of peduncles close to branches. A second mastigophoral spherule may occur at foot of each peduncle, in fosse, especially near directive axis (Fig. 15.) Major outgrowths up to twelve, corresponding to primary and secondary mesenterial cycles. Between major outgrowths smaller ones may be present. Column mostly smooth but small vesicles may occur over 1st- and 2nd-cycle endocoels though their appearance may be due to contraction. Capitulum either withdrawn so that tentacles lie over or among the outgrowths, or fully extended to nearly same height as rest of column. Tentacles up to 48, long, slender, tips blunt, surface granular due to small groups of nematocysts, their size increasing thickness of ectoderm. Disk small, central mouth on top of cone. Height of column to 7 mm, diameter across peduncles 8 mm. *Anatomy*. Mesenteries hexamerously arranged in three cycles, two pairs of directives supporting siphonoglyphs. 1st cycle perfect, fertile. Retractors weak, diffuse, mesogloeal branches thick, with few muscle folds. Parietobasilar muscles weak absent. Basilar muscles present. Weak sphincter found in one specimen but indistinct or absent in all others. Longitudinal muscles of tentacles and radial muscles of disk ectodermal; in sections folds short, mostly unbranched. Ectodermal longitudinal muscle processes on capitulum. Zooxanthellae present in endoderm of column, disk, peduncles and spherules. *Cnidome*. See Table 8 and Figure 16. The size ranges of certain types of nematocysts were found to differ considerably between groups of specimens collected from a single locality, but the cnidome was constant. Nematocysts in tentacles, column and actinopharynx labelled 'b-mastigophores' may be a form of basitrich. *Colour*. Column translucent pale brown with a much darker overlay of small

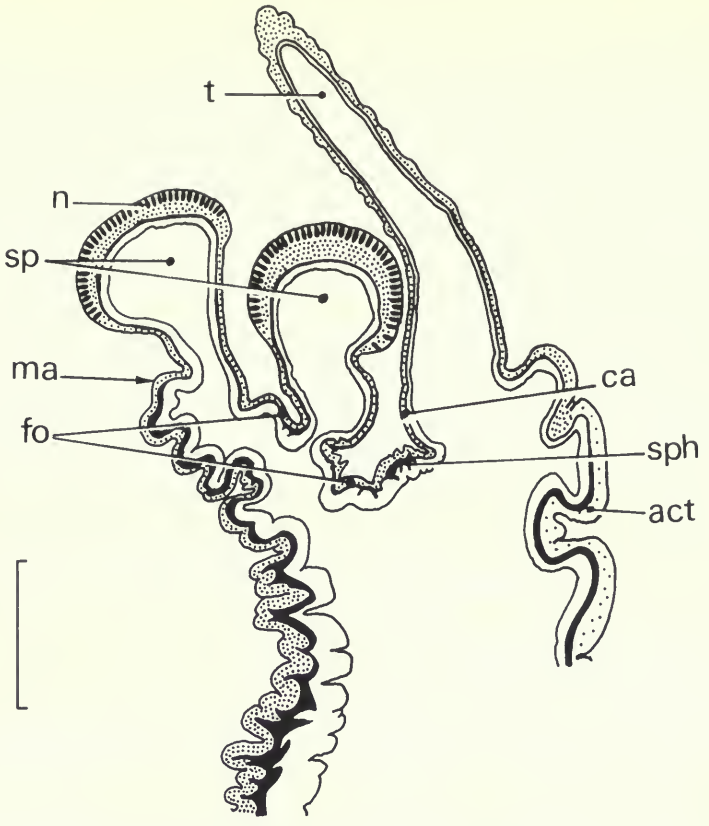

Fig. 15 *Triactis producta*, BMNH 1983.4.8.27. Vertical section through part of column and crown showing two mastigophoral spherules, one on a pedicel from the margin (to left) and one in the fosse (to right), a tentacle, the disk and adjacent actinopharynx. Scale: = 500 μm. (act actinopharynx, ca capitulum, fo base of fosse, ma margin, n nematocysts, sph sphincter, sp spherules, t tentacle. Stippled, ectoderm; black, mesogloea; white, endoderm.)

spots on its lower part grading to continuous beneath peduncles. Capitulum dark brown with pale translucent vertical lines. Tentacles translucent mottled with white, disk pale brown, mouth orange-brown. Upper surfaces of peduncles and fosse with iridescent blue-green sheen over brown ground colour. Spherules white on outer surface, but golden orange within from zooxanthellae.

DISTRIBUTION. Known from several widely spaced localities: Red Sea (Klunzinger, 1877), Maldives (Stephenson, 1921, 1922, as *Phyllodiscus indicus*), Torres Straits (Haddon & Shackleton, 1893 as *Viatrix cincta*), Great Barrier Reef (Carlgren, 1950*b* as *Triactis cincta*), Aden and Singapore (present material).

HABITAT. Usually reported on scleractinian coral, both living and dead. The specimens from Singapore were on *Pavona frondifera* Lamarck (det. Dr S. H. Chuang, University of Singapore). Those from Aden were on similar coral fronds, at depth 2 m, there being several specimens on each.

REMARKS. The presence of branched outgrowths with large mastigophoral spherules on the peduncles (p. 211), and of similar spherules in the fosse, suggests that these specimens should be referred to a species of *Triactis*. The specimens from Aden and Singapore differed slightly, especially in nematocyst size, but the differences are considered too small to justify recognition of two taxa.

Klunzinger (1877) proposed the genus *Triactis* to accommodate *T. producta*, a species from the

Red Sea. His description and illustrations of the species were clear and the specimens from Aden can be referred to it with confidence.

Haddon & Shackleton (1893) collected similar specimens from the Torres Strait and provisionally referred them to the genus *Viatrix* Duchassaing & Michelotti, 1866, under the specific name *V. cincta* Haddon & Shackleton, 1893. Later, following statements by McMurrich (1893, 1896), Haddon (1898) referred the species to the genus *Hoplophoria* Wilson, 1890. According to

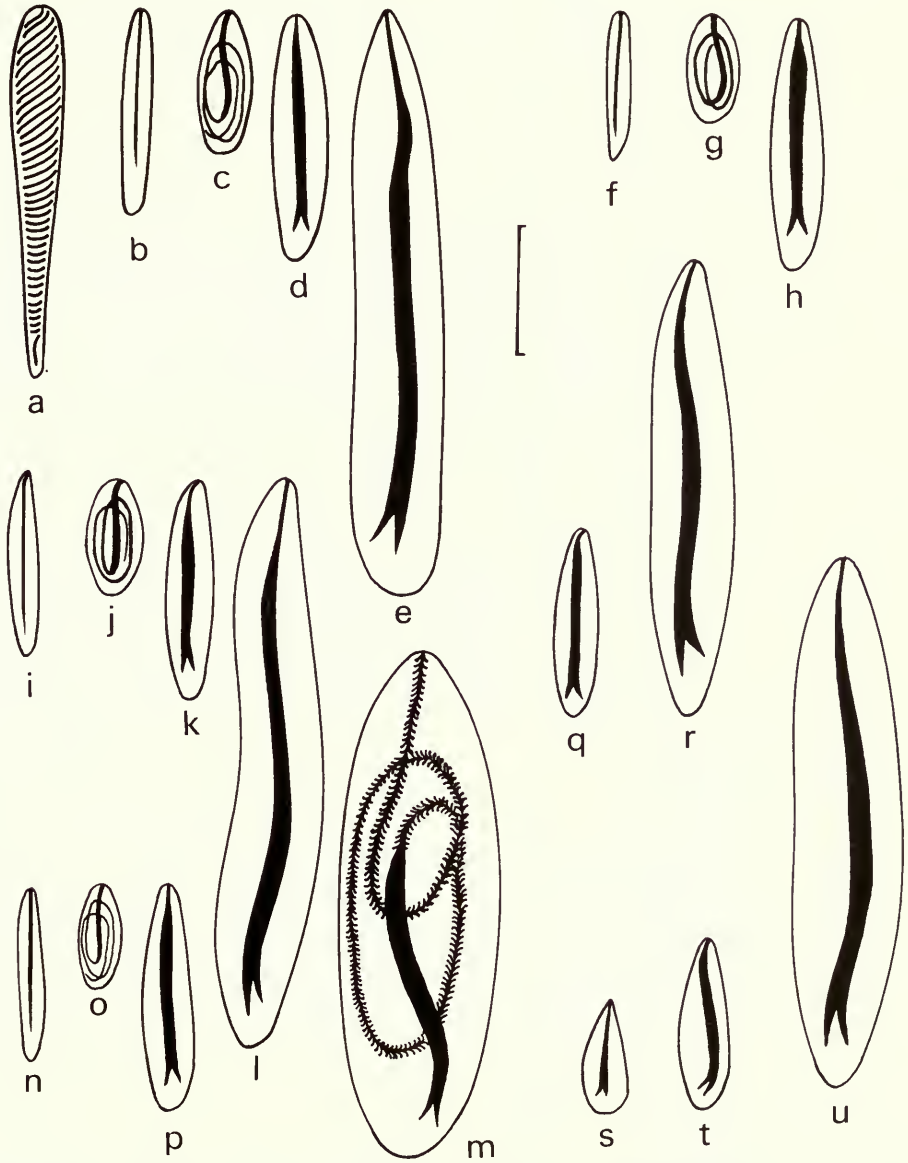

Fig. 16 *Triactis producta*, nematocyst signature (see Table 8). *Tentacle* (a) spirocyst, (b) basitrich, (c) microbasic b-mastigophore, (d-e) microbasic amastigophore. *Column* (f) basitrich, (g) microbasic b-mastigophore, (h) microbasic amastigophore. *Spherules, major* (i) basitrich, (j) microbasic b-mastigophore, (k-l) microbasic amastigophores, (m) macrobasic amastigophore. *Spherules, minor* (n) basitrich, (o) microbasic b-mastigophore, (p) microbasic amastigophore. *Actinopharynx* (q-r) microbasic amastigophores. *Filament* (s-u) microbasic amastigophores. Scale: (a-u) = 10 μm.

Table 8 Size ranges of cnidae of *Triactis producta* (in μm).

Location/ Type of cnida	Localities of specimens			
	Aden (BMNH 1983.4.8.19)	Aden (BMNH 1983.4.8.20)	Singapore (BMNH 1983.4.8.27)	Singapore (BMNH 1983.4.8.25)
Tentacles				
Spirocysts	16·6–37·6 × 2·6–4·0	14·4–37·2 × 2·0–4·8	11·9–46·2 × 2·0–6·7	23·2–33·0 × 2·6–4·6
Basitrichs	13·2–19·9 × 1·5	16·8–19·2 × 2·0	19·9–23·1 × 1·5	9·3–16·6 × 2·0
Microbasic b-mastigophores	9·3–12·0 × 3·3–4·0	9·6–12·0 × 3·6	9·9–16·6 × 3·3–6·0	10·0–11·3 × 3·3
Microbasic amastigophores	10·6–16·6 × 3·3–4·0	14·4–20·4 × 3·6	9·9–28·5 × 3·3–5·3	20·5–31·1 × 4·0
Microbasic amastigophores	29·8–56·7(66·0) × 6·0–6·7	42·0–56·4(72·0) × 6·0–7·2	36·4–64·4(67·3) × 4·6–8·0(9·9)	31·3–56·1(72·8) × 4·6–6·6
Column				
Basitrichs	9·2–11·2 × 1·5	10·6 × 1·5 (3 only)	7·9–9·9 × 1·3	7·2–10·8 × 2·0
Microbasic b-mastigophores	5·3–8·6 × 4·0	8·0–10·0 × 4·6–5·3	6·7–11·2 × 2·6–3·3	7·2–10·8 × 2·6–3·0
Microbasic amastigophores	7·9–19·9 × 2·6–4·0	7·3–25·8 × 3·3–4·0	11·9–19·9 × 2·6–4·0	12·0–34·8 × 3·0–4·8
Spherules-major				
Basitrichs	10·6–19·9 × 2·0	11·3–19·2 × 2·0–2·6	12·0–18·0 × 2·0	8·6–19·2 × 2·0–2·6
Microbasic b-mastigophores	6·6–13·3 × 2·6–4·0	8·6–10·0 × 3·3–4·0	...	5·3–12·0 × 2·0–3·3
Microbasic amastigophores	16·6–25·1 × 4·0–4·6	6·6–26·5 × 3·3–4·0	6·7–28·5 × 2·6–4·6	6·7–27·1 × 2·6–4·6
Microbasic amastigophores	36·4–51·5 × 6·0–6·7	33·0–65·0(78·0) × 5·3–8·0	30·0–63·6(85·0) × 5·4–8·4(10·5)	33·0–59·4 × 4·6–6·6
Macrobasic amastigophores	26·4–39·7 × 8·0–11·9	28·5–39·6 × 9·3–10·6	(33·6)41·6–63·4(71·3) × 11·9–16·6	33·0–59·4 × 9·3–13·3

Spherules-minor				
Basitrichs	9·3–14·6 × 2·0	10·0–15·2 × 2·0	8·0–14·6 × 2·0	10·0–16·6 × 2·0–2·6
Microbasic b-mastigophores	8·0–9·3 × 3·3–4·0	7·3–8·0 × 4·0	8·0–10·6 × 4·0	6·6 × 3·3 (1 only)
Microbasic amastigophores	6·6–22·5 × 2·6–4·0	10·0–27·8 × 3·3–5·3	7·3–26·5 × 2·6–4·0	6·6–25·2(34·3) × 3·3–4·6(6·0)
Actinopharynx				
Microbasic amastigophores	13·3–19·2 × 2·6	10·0–20·0 × 3·3–4·0	11·9–19·9 × 2·6–3·3	12·0–16·8 × 2·4–3·0
Microbasic amastigophores	29·8–39·7 × 4·6–6·0	29·1–41·6 × 5·3–7·3	30·5–49·5 × 4·6–8·0	24·0–42·0 × 3·6–4·8
Filaments				
Microbasic amastigophores	6·7–11·2 × 3·3–4·4	8·0–10·0 × 3·3	7·9–10·6 × 3·3–4·0	6·0–10·8 × 3·0–3·6
Microbasic amastigophores	9·2–18·5 × 3·3–4·0	11·0–21·2 × 3·3–4·0	10·5–16·5 × 2·6–4·0	9·6–15·6 × 2·0
Microbasic amastigophores	23·8–53·5 × 4·0–8·6	36·3–54·0 × 6·0–8·0	50·0–62·0 × 7·3–9·2	39·6–60·0 × 6·0–7·8

Haddon the name *Hoplophoria* was introduced, but not defined, by Wilson (1890) to accommodate an actinian collected in the Bahamas. McMurrich, however, wrote: 'It seems fairly certain that this species is identical with *Viatrix globulifera* originally described by Duchassaing & Michelotti (1860)'. If McMurrich's statement were correct then the genus *Viatrix* Duchassaing & Michelotti, 1866, would take precedence over *Hoplophoria* Wilson, 1890, so why Haddon (1898) employed the later name for the genus is not clear. Still, Haddon's description was adequate to refer his material to the genus *Triactis* (*sensu* Carlgren, 1947) and to identify the specimens from Singapore, shown here to be conspecific with *T. producta* (see below).

Carlgren (1950*b*), after studying material from Low Island, suggested that *Triactis cinctus* and *T. producta* were conspecific. This suggestion is confirmed from the present study of specimens from Aden and Singapore. The species name *T. producta* Klunzinger, 1877, has priority over *T. cincta* (Haddon & Shackleton, 1893) and is employed here.

Phyllodiscus indicus Stephenson, 1921, is here considered conspecific with *Triactis producta*. When first described the species was referred to *Phyllodiscus* Kwietniewski, 1897, but only provisionally since the anatomy of *Triactis* was incompletely known. Stephenson included in the same genus *P. semoni* Kwietniewski, 1897: 407, and *Hoplophoria cincta* (Haddon & Shackleton, 1893: 127). Stephenson's description of *P. indicus* and his illustration (Stephenson, 1921, Fig. 18) show that his concept of *Phyllodiscus* is identical with *Triactis* sensu Klunzinger. However, *Phyllodiscus* Kwietniewski, 1897, is regarded as valid and *P. semoni* is not referred to *Triactis* (following Carlgren, 1924: 11).

Family **ACTINIIDAE** (Rafinesque, 1815)

NOMENCLATURE. Williams, Cornelius & Clark (1982), in proposing validation of the family name Actiniidae, considered that the earliest use of this family name was by Goldfuss (1820). However, L. B. Holthuis of Leiden has since informed the International Commission on Zoological Nomenclature of an earlier use, by Rafinesque (1815: 155) (Holthuis, Opinion 1295, *Bulletin of Zoological Nomenclature* 42: 34–36). The family name has been validated by the Commission. Dating of the Rafinesque work follows Iredale (1911).

Genus ***ANTHOPLEURA*** Duchassaing & Michelotti, 1860

Actinia (Isacmaea) Ehrenberg, 1834: 34 (part).
Tarastephanus Brandt, 1835: 1 (part).
Monostephanus Brandt, 1835: 10 (part).
Cereus: Milne Edwards, 1857: 266.
Bunodes: Gosse, 1855: 274; Gosse, 1860: 195, 198; Johnson, 1861: 302; Klunzinger, 1877: 77; Andres, 1881: 318; Andres, 1883: 423; Pennington, 1885: 167; Dixon, 1889: 310; Duerden, 1898: 454; Carlgren, 1898: 19; Carlgren, 1900: 66; Stuckey, 1908: 368; Fischer, 1889: 301 (part).
Isacmaea: Milne Edwards, 1857: 288.
Anthopleura Duchassaing & Michelotti, 1860: 49; Duchassaing & Michelotti, 1866: 126; Andres, 1883: 440.
Aegeon Gosse, 1865: 41.
Evactis Verrill, 1969*b*: 470; Andres, 1883: 446.
Actinioides Haddon & Shackleton, 1893: 126; Haddon, 1898: 424; Kwietniewski, 1897: 33 (389); Duerden, 1898: 453; Carlgren, 1900: 63; Carlgren, 1938: 32; Pax, 1907: 79; Pax, 1908: 490.
Isactinia Carlgren, 1900: 53.
Cribrina: McMurrich, 1901: 18; McMurrich, 1904: 287; Pax, 1908: 474.
Bunodactis: Pax, 1920: 31; Pax, 1926: 23; Stephenson, 1921: 529; Stephenson, 1922: 271.
Tealiopsis: Verrill, 1922: 110; Verill, 1928: 26.
Anthostella Carlgren, 1938: 38.

NOMENCLATURE. The generic name *Anthopleura* Duchassaing & Michelotti, 1860, is used here following the practice of Carlgren (1949), Stephenson (1935) and Manuel (1981).

DEFINITION. Actiniidae with well developed pedal disk. Column with adhesive verrucae arranged in more or less distinct vertical rows especially in the upper part. *Heterotrichs present in*

column ectoderm. Atrichal marginal spherules present *or atrichal spherules in fosse*. Atrichs suppressed here in some specimens. Sphincter weak to strong, endodermal, diffuse to circumscribed. Tentacles simple, hexamerously or irregularly arranged, longitudinal muscles ectodermal or meso-ectodermal. Numerous perfect mesenteries, all stronger ones fertile. About the same number of mesenteries distally and proximally but, since mesenteries grow from base upwards in some species, a few more may be found proximally. Retractors of stronger mesenteries diffuse, sometimes restricted. Cnidome: spirocysts, atrichs, heterotrichs, basitrichs and microbasic amastigophores.

TYPE SPECIES. *A. krebsi* Duchassaing & Michelotti, 1860, by monotypy.

REMARKS. The characteristic nematocysts of the marginal spherules are a distinctive feature of the genus *Anthopleura*. They are usually referred to as atrichs but are possibly of two types, atrichs and heterotrichs. *Anthopleura* spp. lacking atrichs and heterotrichs in the spherules are provisionally assigned to the genus. Examples are *Anthopleura dixoniana* (Haddon & Shackleton, 1893) and *A. handi* Dunn, 1977, redescribed here. Species lacking atrichs in the spherules but having other characters of *Anthopleura* were often mistakenly assigned to the genus *Bunodactis* (now referred to the genus *Aulactinia,* see Dunn, Fu-Shiang Chia & Levine, 1980: 2078, also p. 255). The best character by which *Anthopleura* can be distinguished from *Bunodactis* is the presence of heterotrichs in the ectoderm of the column. They are not found in species referred to *Bunodactis*, *Aulactinia* or *Gyractis*. Their reported occurrence is listed in Table 9. It is interesting that Schmidt (1972: 91–92) did not find them in *A. balli* (Cocks, 1851) from the Mediterranean, nor Carlgren when first describing *A. sanctaehelenae* Carlgren, 1941: 4, and the generic affinity of these species needs re-appraisal. The distinctive heterotrichs of the column (see Figs 19h, 21h, 23h, and 25h) should not be confused with the atrichs that sometimes occur only at the limbus in certain

Table 9 *Anthopleura* spp. having heterotrichs in column ectoderm.

Species	Nematocyst referred to as:	Source of data
A. annae Carlgren, 1940*b*	Atrichs	Carlgren, 1940*b*: 4
A. artemisia (Pickering in) Dana, 1846: 38	Atrichs	Hand, 1955: 65, Fig. 15
A. asiatica Uchida & Muramatsu, 1958	Holotrichs	Uchida & Muramatsu, 1958: 118, Fig. 5
A. aureoradiata (Stuckey, 1909)	Atrichs	Carlgren, 1950*c*: 4
A. dixoniana (Haddon & Shackleton, 1893)	Heterotrichs	England (see p. 242)
A. elegantissima (Brandt, 1835)	Atrichs	Hand, 1955: 59, Fig. 13
A. handi Dunn, 1977	Atrichs	Dunn, 1977: 8
A. hermaphroditica Carlgren, 1898	Atrichs	Carlgren, 1959: 22
A. insignis Carlgren, 1940*b*	Atrichs (limbus only?)	Carlgren, 1940*b*: 4
A. krebsi Duchassaing & Michelotti, 1860	Atrichs	Carlgren & Hedgepeth, 1952: 154
A. kurogané Uchida & Muramatsu, 1958	Holotrichs	Uchida & Muramatsu, 1958: 114, Fig. 2
A. michaelseni (Pax, 1920)	Atrichs	Carlgren, 1938: 45
A. midori Uchida & Muramatsu, 1958	Holotrichs	Uchida & Muramatsu, 1958: 112, Fig. 1
A. mortenseni Carlgren, 1941	Atrichs	Carlgren, 1941: 3
A. nigrescens (Verrill, 1928)	Heterotrichs	England (see p. 249)
A. orientalis Averincev, 1967	Atrichs	Averincev, 1967: 70
A. pacifica Uchida 1938	Basitrichs/heterotrichs	Uchida & Maramatsu, 1958: 116, Fig. 3
A. pannikkarri Parulekar, 1968	Holotrichs	Parulekar, 1968: 590–595
A. rubripunctata (Grube, 1840)	Haplonemes	Schmidt, 1972: 89
A. stellula (Ehrenberg, 1834)	Haplonemes	Schmidt, 1970: 24
A. varioarmata Watzl, 1922	Atrichs	Carlgren, 1952: 374
A. waridi (Carlgren, 1900)	Heterotrichs	England (see p. 252)
A. xanthogrammica (Brandt, 1835)	Atrichs	Hand, 1955: 52, Fig. 11

*Uchida & Maramatsu list basitrichs but illustrate heterotrichs.

anemones, but usually in large numbers, as for example in *Epiactis prolifera* Verrill, 1869*b* (personal observation), *Bunodactis maculosa* Carlgren, 1954, and *Isanemonia australis* Carlgren, 1950*c*.

Anthopleura dixoniana (Haddon & Shackleton, 1893)
Figs 17–19

Actinioides dixoniana Haddon & Shackleton, 1893: 126; Haddon, 1898: 424–426, pl. 22, fig. 6, pl. 27, figs 1–2.
Actinioides papuensis Haddon, 1898: 426–428, pl. 22, fig. 7, pl. 27, figs 3–7.
Actiniogeton papuensis: Carlgren, 1949: 62.
Anthopleura dixoniana: Carlgren, 1938: 32; Carlgren, 1949: 54.

Material Examined. Singapore: Changi Creek, 50 specimens, 16 Feb 1970 BMNH 1983.8.4.1–50; Pungol Point, 26 specimens, 19 May 1970, BMNH 1983.8.4.51–77; Pasir Panjang, 9 specimens, 24 Jun 1970, BMNH 1983.8.4.76–85. Torres Strait: Mabuaing, 2 specimens, coll. A. C. Haddon, Cambridge University Zoological Museum, Co177 (in jar labelled *Actinioides sesere*). Specimens also examined from Hong Kong and Gan, Addu Atoll, Maldives.

Description. Column tall, height about twice diameter when extended, upper part with vertical rows of small prominent verrucae, each row topped at margin by a large spherule that may or may not be atrichal; but some specimens lacking atrichal marginal spherules. Spherules simple or compound with nematocyst batteries, when present, located on top and inner faces. Verrucae extending onto outer surfaces of spherules. Tentacles varied in number, up to 60, slender, tapered, in two circlets, inner longer than outer. Disk flat; base present. *Anatomy*. 3–8 siphonoglyphs seen, each supported by directives. Number of mesenteries varied but most are perfect; number of tentacles same as number of mesenteries at base of column (Table 10). Typical arrangements of mesenteries in apparent cycles are shown in Figure 17. Mesenteries apparently in three cycles but not hexamerously arranged, all or most of the 1st cycle being directives. Retractor muscles weak-diffuse; parietobasilar muscles weak with free inner edge. Sphincter weak-diffuse to circumscribed and varied between specimens (Fig. 18). Marginal spherules endocoelic; mostly atrichal, some lacking atrichs interspersed irregularly with atrichal spherules. Zooxanthellae present. Largest specimen, height 10 mm, diameter 10 mm. *Cnidome*. See Table 11 and Figure 19. *Colour*. Column either pale green to yellowish green near limbus, becoming grey towards margin, covered with small yellow spots; or deep brown near the limbus becoming pale greenish white above with white vertical lines. Marginal spherules green or brown with orange-brown or golden-yellow spots or patches (atrichal regions). Verrucae grey. Tentacles with brownish tint on upper surface broken by 2–4 translucent white elliptical patches. Disk brown, tinged with green and yellow around the mouth and with cream or white patches over the endocoels.

Table 10 *Anthopleura dixoniana*. Relation between numbers of tentacles, mesenteries, directivies, siphonoglyphs and spherules. Each line of the table represents one specimen.

Tentacles	Mesenteries at base	Directive mesenteries	Siphonoglyphs	Spherules
18	9 pairs	3 pairs	3	8
21	10 pairs	4 pairs	4	11
34	17 pairs	5 pairs	5	...
38	19 pairs	5 pairs	5	20
39	19 pairs + 1	6 pairs	6	20
42	22 pairs	5 pairs	5	19
62	...	5 pairs	5	20

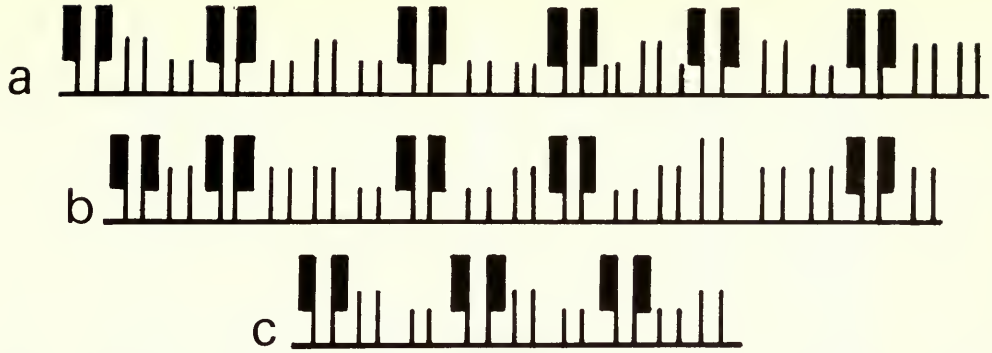

Fig. 17 *Anthopleura dixoniana* Complete mesenterial arrangements of 3 specimens. (a) BMNH 1983.8.4.1; (b) BMNH 1983.8.4.2; (c) BMNH 1983.8.4.4. (black rectangles = directive mesenteries.)

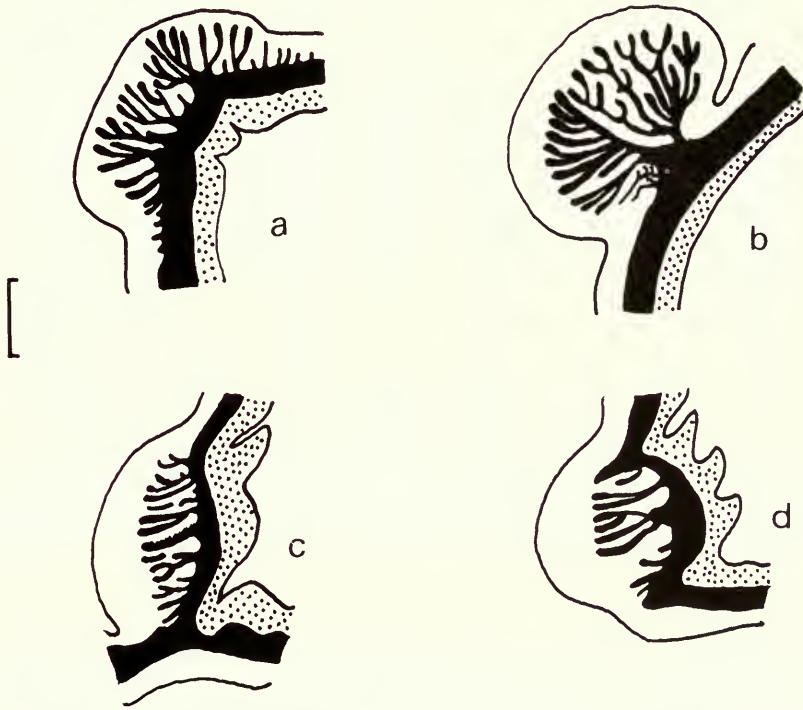

Fig. 18 *Anthopleura dixoniana* Vertical sections of two specimens to show variation of sphincter muscle. (a-b) Singapore, BMNH 1983.8.4.51; (c-d) Singapore, BMNH 1983.8.4.1. Scale: (a-b) = 65 μm, (c-d) = 30 μm. (Stippled, ectoderm of fosse; black, mesogloea; white, endoderm.)

DISTRIBUTION. Recorded from Torres Strait (Haddon & Shackleton, 1893, as *Actinioides dixoniana* and *A. papuensis*), the Maldives, Singapore, and Hong Kong (present material).

HABITAT. In holes in rocks and stones; many specimens aggregating in a small area, but not close to each other; upper shore.

REMARKS. The presence of atrichal marginal spherules, verrucae on the column, and a uniform number of mesenteries at margin and base, place this species in the genus *Anthopleura*. The varied

Table 11 Size ranges of cnidae of *Anthopleura dixoniana* (in μm).

Location/ Type of cnida	Identity of specimens from Singapore				
	(BMNH 1983.8.4.51)	(BMNH 1983.8.4.52)	(BMNH 1983.8.4.76)	(BMNH 1983.8.4.77)	(BMNH 1983.8.4.78)
Tentacle					
Spirocyst	9·8–20·8 × 2·0–2·3	10·8–20·4 × 2·0–3·6	10·0–22·5 × 1·8–2·4	16·8–24·0 × 2·4–3·0	12·0–21·6 × 2·4–3·0
Basitrich	13·0–16·3 × 2·0	12·0–18·0 × 2·0–2·4	16·2–20·0 × 2·4	14·4–19·2 × 2·4–3·0	13·2–18·0 × 1·8–2·4
Column					
Basitrich	11·1–13·7 × 2·0	12·0–14·4 × 2·4	12·5–16·2 × 1·8	11·0–16·8 × 2·4–3·0	10·8–13·2 × 1·8–2·4
Heterotrich	11·1–14·3 × 3·3–4·6	11·4–15·6 × 3·6–4·2	12·5–16·2 × 3·7	13·2–18·0 × 3·6–4·2	12·0–15·6 × 3·0–3·6
Marginal Spherule					
Spirocyst	16·3–26·0 × 2·0–2·6	19·5–28·0 × 2·0–2·6	21·2–25·0 × 1·8	18·0–32·4 × 2·0–2·4	. . .
Basitrich	9·1–10·4 × 1·3	9·6–11·1 × 1·3	11·2–13·7 × 1·2–1·8	10·8–14·4 × 1·2–1·8	8·4–13·0 × 1·8
Heterotrich	24·7–33·8 × 2·6–3·3	25·4–37·0 × 2·0–4·0	31·2–42·5 × 3·7–4·8	27·6–44·4 × 3·0–4·2	. . .
Atrich	26·0–35·8 × 3·3–4·6	26·0–35·8 × 3·3–4·6	32·5–42·5 × 3·7–4·8	28·8–48·0 × 3·7–6·0	. . .
Actinopharynx					
Basitrich	11·1–13·7 × 2·0–2·6	12·0–20·4 × 2·4–3·0	9·6–14·4 × 1·8–2·4	9·6–12·0 × 1·8	9·6–18·0 × 1·8–2·4
Basitrich	14·3–21·5 × 2·6–3·3	. . .	15·6–26·4 × 2·4–3·0	19·2–27·6 × 2·4–3·0	12·0–21·6 × 2·4–3·0
Microbasic amastigophore	16·6–19·5 × 4·0	18·0–20·4 × 3·6–4·8	16·2–21·6 × 3·6–4·8	15·6–20·4 × 3·6–4·8	15·6–19·2 × 3·6–4·8
Filament					
Basitrich	9·8–13·0 × 1·3	9·8–13·2 × 1·2–1·8	9·6–16·8 × 1·8	10·8–18·0 × 1·8	9·6–15·6 × 1·8
Basitrich	20·2–26·7 × 4·0–4·6	21·6–27·6 × 3·6–5·4	21·6–32·4 × 3·6–4·8	21·6–28·8 × 2·4–3·0	19·2–26·4 × 4·2–5·4
Microbasic p-mastigophore	10·4–13·0 × 3·3	10·8–13·2 × 3·0–3·6	12·0–14·4 × 2·4–3·0	12·0–15·6 × 2·4–3·0	10·8–14·4 × 2·4–3·6
Microbasic amastigophore	16·3–21·5 × 3·3–4·6	16·8–21·6 × 3·0–4·2	16·8–22·8 × 3·6–4·8	16·8–21·6 × 3·0–4·8	12·0–20·4 × 3·0–6·0

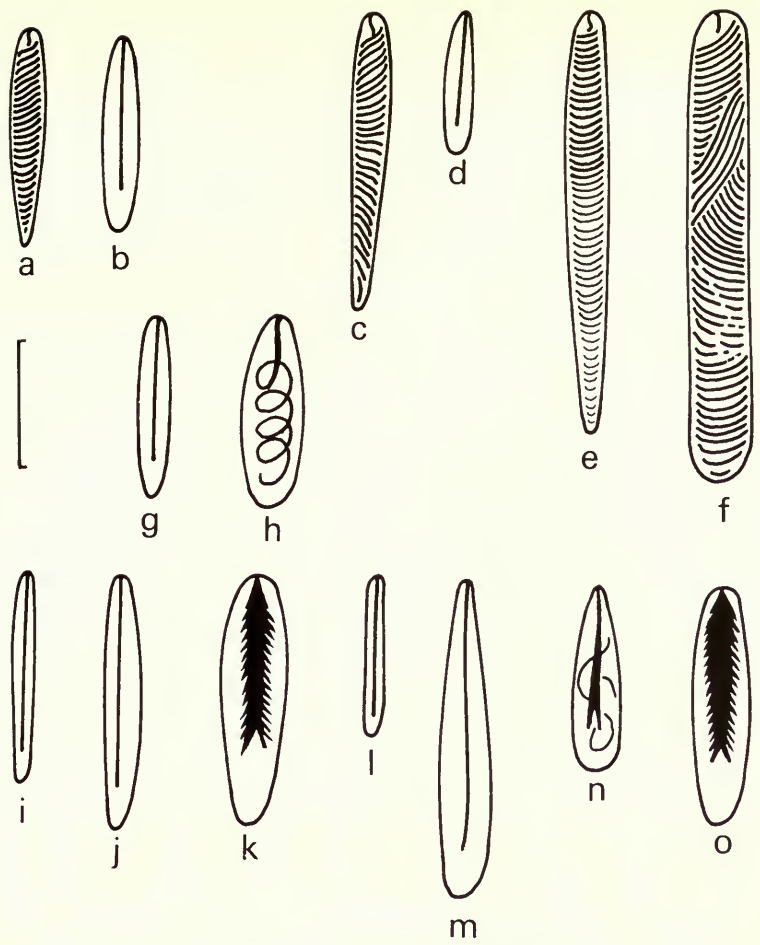

Fig. 19 *Anthopleura dixoniana*, nematocyst signature (see Table 11). *Tentacle* (a) spirocyst, (b) basitrich. *Marginal spherule* (c) spirocyst, (d) basitrich, (e) heterotrich, (f) atrich. *Column* (g) basitrich, (h) heterotrich. *Actinopharynx* (i-j) basitrichs, (k) microbasic amastigophore. *Filament* (l-m) basitrichs, (n) microbasic p-mastigophore, (o) microbasic amastigophore. Scale: (a-o) = 10 μm.

number of siphonoglyphs supported by directives recalls the genus *Actinioides* Haddon & Shackleton, 1893, proposed to accommodate the then newly described *A. dixoniana, A. papuensis* and *A. sesere*. The first two were distinguished purely on sphincter character and colour. Both species were stated by Haddon (1898) to have several siphonoglyphs, all supported by directives. *A. sesere* was separated from the others again on the character of the sphincter, but it is not clear from the description if the *A. sesere* material had many siphonoglyphs. The Pasir Panjang specimens had a sphincter similar to that illustrated by Haddon (1898, pl. 27, fig. 1; see Fig. 18b) in *A. dixoniana*, and had several siphonoglyphs supported by directives. No other species of *Anthopleura* has been reported with these characters, but see *A. waridi* (p. 250) which differs from the present material in having the atrichal spherules in the fosse and not on the margin. It is thus apparent that the specimens are referable to *A. dixoniana*. The Changi Creek specimens, although smaller than the others, had a sphincter similar to that in *A. papuensis* and can be referred to this species. The specimens from Pasir Panjang and Pungol Point had sphincters similar to those of *A. dixoniana*. Examination of the nematocysts of these two species, however, showed no difference in either type

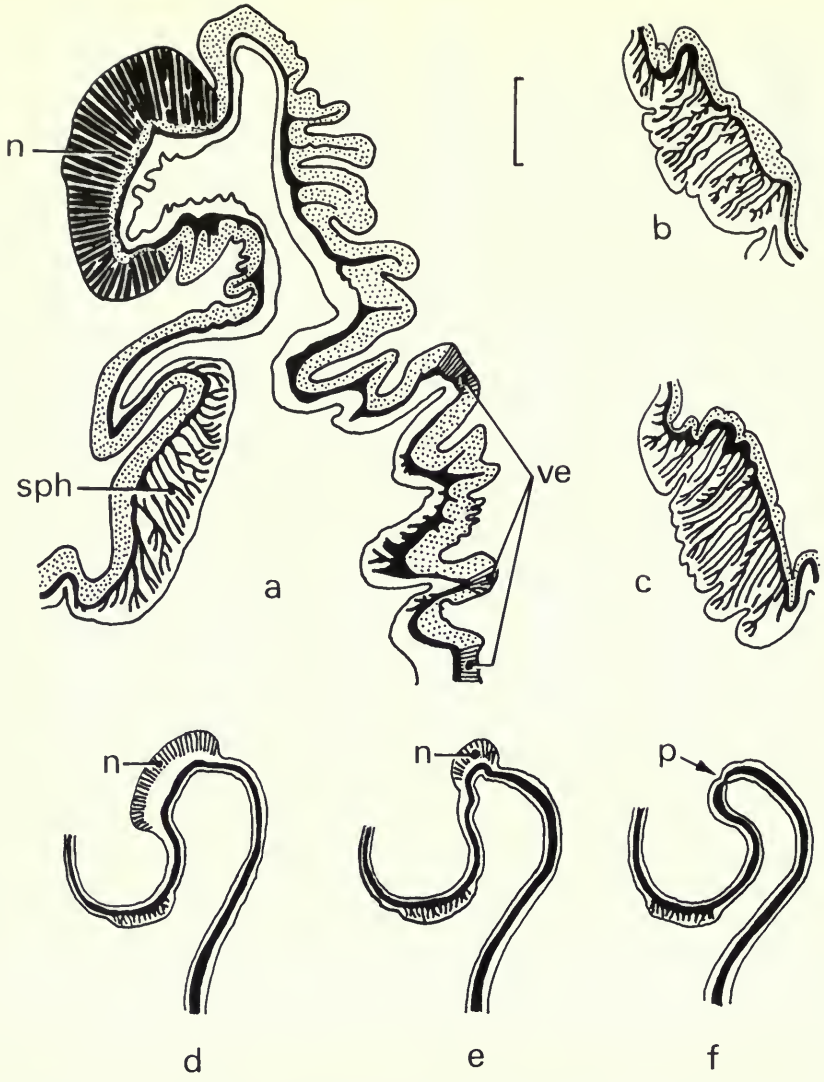

Fig. 20 *Anthopleura handi.* (a) Vertical section through margin showing spherule and sphincter, BMNH 1983.8.24.51. (b-c) Difference between sphincter muscles in vertical section of two other specimens. (d-e) Extremes of size of nematocyst batteries on atrichal marginal spherules. Scale: (a-c) = 10 μm, (d-f) arbitrary. (n nematocysts, p pore, sph sphincter, ve verrucae. Stippled, ectoderm; black, mesogloea; white, endoderm.)

or size range (Table 11). The sphincter, in section, could differ between specimens. A range from weak-diffuse to fairly strong restricted sphincter muscles was found in both *A. dixoniana* and *A. papuensis*. Hence *A. papuensis* can be confidently referred to *A. dixoniana*.

Haddon's original specimens labelled *A. sesere*, preserved in Cambridge University Zoological Museum, comprised two species in one jar. Most were certainly '*A. sesere*' (now referred to *Gyractis excavata,* p. 255), but two specimens were identified as *A. dixoniana*. One of these had eight pairs of directives supporting eight siphonoglyphs among twenty-six pairs of mesentries.

Carlgren (1938: 32), when placing the similar species *Actiniogeton sultana*, suggested that *Actinioides dixoniana* should be referred to *Anthopleura*, especially since Haddon had depicted

large acrorhagi. Carlgren stated that if the marginal spherules of *A. dixoniana* were true acrorhagi, and if more mesenteries were present at the base than at the margin, the species should be referred to *Anthopleura* and the genus *Actinioides* would lapse. *A. dixoniana* clearly possesses atrichal marginal spherules (true acrorhagi), but the number of mesenteries is about the same distally and proximally. However, since this is true of nearly all species of *Anthopleura* a difference of only a few more mesenteries at margin or base is of no consequence (p. 214). Hence *Actinioides* should be referred to *Anthopleura*. The present specimens are, therefore, referred to *Anthopleura dixoniana* with which *A. papuensis* is conspecific.

Anthopleura handi Dunn, 1977
Figs 20–21

?*Anthopleura hermaphroditica* Carlgren, 1898: 23, fig. 18; Carlgren, 1921: 148; Carlgren, 1927: 32; Carlgren, 1949: 54, pl. 2, fig. 2; Carlgren, 1959: 22.
Anthopleura handi Dunn, 1977: 54–64, figs 1–8.

Material Examined. Singapore: Pasir Ris, 15 specimens, 24 Mar 1970 BMNH 1983.8.24.51–60.

Description. Column tall when extended, mostly smooth but with small inconspicuous verrucae near margin continuing onto marginal spherules. Marginal spherules haphazardly arranged, large to small (Figs 20a, d, e). Some spherules with atrichs but usually without. Tentacles tapered, smooth, in two circlets, inner slightly longer than outer. Disk flat; mouth large; two distinct siphonoglyphs. Base slightly smaller in diameter than disk. *Anatomy*. Sphincter diffuse (Fig. 20a-c). Mesenteries hexamerously arranged in up to four cycles; first three cycles perfect and fertile, including directives; 4th cycle incomplete, usually without filaments. Retractor muscles weak, diffuse, restricted in contraction; mesogloeal folds much branched. Parietobasilar muscles prominent, inner edge detached from mesentery. Basilar muscles present. Two well developed siphonoglyphs supported by directives. Usually same number of mesenteries distally and proximally but sometimes with additional mesenteries at either base or disk. Four specimens examined had arrangements shown in Table 12. Although verrucae often indistinct in life, in histological

Table 12 *Anthopleura handi*. Relation between numbers of tentacles, mesenteries at disk and base and spherules in four specimens (BMNH 1983.8.24.51–60).

	Mesenteries		
Tentacles	Disk	Base	Spherules
50	50	...	25
50	50	58	24
54	54	58	24
69	70	64	30

section structure can be seen. Imperforate cinclides located at centre of column in primary endocoels, up to 6 cinclides in a vertical row; arising as endodermal invaginations. Dioecious; broods, two embryos found in enteron of one specimen. Zooxanthellae not found. *Cnidome*. See Table 13 and Figure 21. *Colour*. Specimens from Pasir Ris were white. See Dunn (1977: 54–55) for other colour varieties.

Distribution. Malaysia (Dunn, 1977) and Singapore (present material).

Habitat. Attached to mussels in sand, MLTL.

Table 13 Size ranges of cnidae of *Anthopleura handi* and *A. hermaphroditica* (in μm).

Location/ Type of cnida	Localities of specimens				
	Singapore (BMNH 1983.8.24.51)	Singapore (BMNH 1983.8.24.52)	Singapore (BMNH 1983.8.24.53)	Hawaii (Dunn 1977: 57–59)	Chile *A. hermaphroditica* (after Carlgren, 1959: 22)
Tentacle					
Spirocyst	11·8–22·4 × 1·8–3·5	13·0–21·2 × 2·4–3·6	11·3–19·9 × 1·4–2·6	9·9–24·3 × 2·1–3·7	. . .
Basitrich	14·1–23·6 × 1·8–2·4	17·7–22·4 × 2·4	15·9–21·8 × 2·4	15·3–24·7 × 1·8–3·6	21·0–24·0 × 2·8–3·0 (15·5–18·3)
Column					
Basitrich	9·4–16·5 × 1·8	10·6–15·3 × 1·8	13·3–16·5 × 1·8	11·7–20·7 × 1·8–3·1	17·0–24·0 × 2·8–3·5 (14·0–15·5)
Heterotrich	15·3–22·4 × 3·6–4·2	16·5–18·9 × 3·0–4·2	14·2–23·3 × 3·0–4·2	18·0–28·8(34·2) × 2·7–4·1(4·5)	19·7–31·0 × 4·2–6·3 (14·0–15·5)
Marginal Spherule					
Spirocyst	. . .	17·7–29·5 × 1·8–2·4	19·9–23·2 × 2·0–3·3	12·4–24·3 × 1·8–4·1	. . .
Basitrich	8·2–15·3 × 1·8	11·8–14·2 × 1·8	16·6 × 2·0 (1 only)	10·8–20·6(25·2) × 1·6–3·6	. . .
Heterotrich	Absent	29·5–43·6 × 3·0	31·8–48·2 × 2·6–4·0	27·0–43·3(50·4) × 3·2–4·5(6·3)	39·5–51·0 × 5·0–5·6 (28·2–35·2)
Atrich	Absent	38·9–49·5 × 3·6–4·8	39·6–46·2 × 4·0–4·6		
Actinopharynx					
Basitrich	11·8–17·7 × 1·8	11·8–14·2 × 1·8	13·2–14·6 × 1·8	(16·5)19·6–30·6(33·0) × 2·1–3·7	22·6–28·2 × 4·0–5·0 (. . .)
Basitrich	20·0–24·8 × 2·4–3·0	15·3–26·0 × 2·4–3·0	15·3–23·8 × 2·0		
Microbasic amastigophone	17·7–21·2 × 3·6–5·8	15·3–20·0 × 4·2–4·7	13·2–19·9 × 3·3–4·0	16·5–22·7(24·7) × 4·1–6·2	21·0–24·0 × 4·2–4·5 (. . .)
Filament					
Basitrich	10·6–11·8 × 1·2	8·2–10·6 × 1·2	. . .	8·2–20·0 × 1·8–3·2	. . .
Basitrich	26·0–33·0 × 3·6–4·7	23·6–29·5 × 3·6–4·8	21·2–29·8 × 3·0–3·6	24·3–37·1(39·1) × 3·2–5·4	24·0–35·2 × 4·2–5·6 (24·0–29·6)
Microbasic p-mastigophore	11·8–15·3 × 3·0	11·8–17·7 × 2·4–3·0	10·6–14·2 × 2·4	(14·4)16·5–24·7 × (2·5)3·6–7·2)	19·7–25·4 × 4·2–7·0 (18·3–21·0)
Microbasic amastigophore	18·9–21·2 × 4·0	15·3–20·0 × 3·0–5·8	14·0–18·9 × 3·6–4·7)		

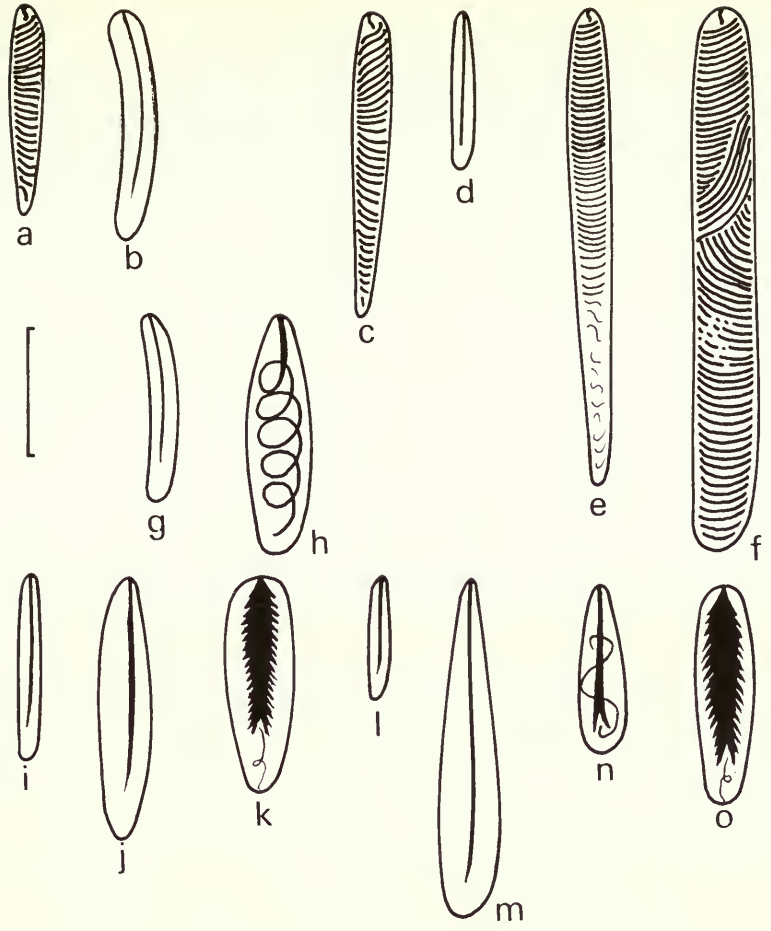

Fig. 21 *Anthopleura handi*, nematocyst signature (see Table 13). *Tentacle* (a) spirocyst, (b) basitrich. *Marginal spherule* (c) spirocyst, (d) basitrich, (e) heterotrich, (f) atrich. *Column* (g) basitrich, (h) heterotrich. *Actinopharynx* (i-j) basitrichs, (k) microbasic amastigophore. *Filament* (l-m) basitrichs, (n) microbasic p-mastigophore, (o) microbasic amastigophore. Scale: (a-o) = 10 μm.

Remarks. The verrucated column and the atrichal marginal spherules suggest that this species is best referred to *Anthopleura*. Of the many included species only three or four have been found to brood, *A. hermaphroditica* Carlgren, 1898), *A. aureoradiata* (Stuckey, 1909; see Carlgren, 1950*c*: 4), *Anthopleura* sp. Atoda, 1945: 274, and *A. handi* Dunn, 1977: 54).

In the present material the mesenterial arrangement, sphincter characteristics and nematocyst data were as reported by Dunn in *A. handi*. There were in addition cinclides in the centre of the column and both atrichs and heterotrichs in the marginal spherules (Table 13 and Figure 21). The size ranges of the cnidae differed only slightly from those in Dunn's account and need not be considered further.

Dunn suggested that *A. handi* differed from *A. hermaphorditica* in having the sphincter diffuse, not well developed and circumscribed. Carlgren stated that the sphincter was circumscript with a tendency to become mesogloeal near its base, but his illustration (1949, pl. 2, fig. 2) appears to show a circumscript sphincter. The section was probably taken from the region where the sphincter passed through the mesentery, where the muscle folds of the sphincter and mesenteric retractor or

transverse muscles might have interwoven. This might account for Carlgren's conclusion that the sphincter tended to become mesogloeal. The plane of section might account for a lamella of mesogloea between the sphincter and the column mesogloea, the sphincter in reality being diffuse. The sphincter of *A. hermaphroditica* is similar to that of *A. handi* (Figs 20a, b, c) but appears much larger. Carlgren's specimens of *A. hermaphroditica* should be re-examined.

Carlgren (1959: 22) gave the nematocyst size ranges in two specimens of *A. hermaphroditica*. In one specimen they were close to those found by Dunn and myself, but the ranges of his second specimen were so different, particularly in tentacles and column, as to suggest a distinct species. Comparison of the size ranges of this specimen with those of *Bunodactis hermaphroditica* (*sensu* Carlgren, 1959: 23) suggests that it belongs to that species. The presence of atrichs, however, precludes *Bunodactis*. The question arises as to whether *B. hermaphroditica* is best referred to *Bunodactis* or should be considered within the scope of *Anthopleura* but with the atrichs of the marginal spherules absent or suppressed (p. 239).

Carlgren stated that *A. hermaphroditica* is hermaphrodite but male gonads were not seen in the present specimen. Two specimens had young in the enteron as well as eggs on the gonads.

The only differences recorded here between *A. handi* and *A. hermaphorditica* are the presence of cinclides in *A. handi* and its considerably fewer tentacles. Carlgren reported a maximum of 90 tentacles in *A. hermaphroditica* whereas Dunn found a maximum of 61 in 200 specimens of *A. handi* and a maximum of 69 was found in the present material.

It seems best to recognize provisionally both *A. handi* and *A. hermaphroditica* until Carlgren's material can be re-examined and the identity of the latter established.

Anthopleura nigrescens (Verrill, 1928)
Figs 22–23

Tealiopsis nigrescens Verrill, 1928: 26, pl. 5A-B.
Bunodactis nigrescens: Carlgren, 1949: 65.
Anthopleura nigrescens: England, 1969: 5; Dunn, 1974*a*: 377–382, figs 1–4.

Material Examined. Holotype: United States National Museum of Natural History,

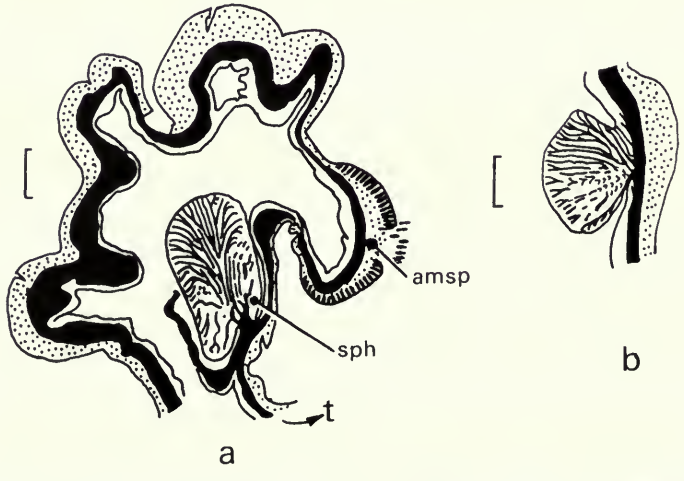

Fig. 22 *Anthopleura nigrescens* (United States National Museum 209154). (a) Vertical section through margin showing position of an atrichal marginal spherule and strong circumscribed sphincter. (b) Vertical section of restricted diffuse sphincter of a smaller specimen. Scale: (a) = 200 μm, (b) = 100 μm. (amsp atrichal marginal spherule, sph sphincter. Stippled, ectoderm; black, mesogloea; white, endoderm.)

Washington D.C., 1925–1485. Paratype: American Museum of Natural History 1480. Hawaii: 2 specimens, coll. C. E. Cutress, 1955, USNM 209154; 3 specimens, coll. D. F. Dunn (pers. coll.). Hong Kong: 2 specimens, coll. B. Morton, 20 Mar 1981. India: Cochin, coll. Kuruvilla Matthew, 1968, BMNH 1983.8.4.86. Australia: North Queensland, 2 specimens, coll. R. Muffley, James Cook University, Townsville, Queensland.

DESCRIPTION. See Dunn (1974*a*: 377–382, figs 1–4).

DISTRIBUTION. Hawaii (Verrill, 1928 as *Tealiopsis nigrescens*, Cutress, 1955 and Dunn, 1974*a*); Hong Kong, Queensland, and India (present material).

REMARKS. The species is readily identified by the heavily verrucated column, the prominent atrichal marginal spherules and the irregularly arranged mesenteries with several siphonoglyphs never supported by directive mesenteries. The spherules are normally large with verrucae on the outer face. The large nematocyst batteries are located on the crown of the spherule, often turned into the fosse, and are easily distinguished even in preserved material. Usually all spherules are atrichal. The sphincter varied from restricted-diffuse (Fig. 22b) to strong-circumscribed (Fig. 22a), and was frequently larger than indicated by Dunn (1974*a*). The sphincter of the holotype is strong-circumscribed, similar to Figure 22a. Dunn recorded 80 tentacles in samples from a Hawaiian population but a specimen from the present material has as many as 167. *Cnidome*. See Table 14 and Figure 23. The size ranges are slightly larger than those quoted by Dunn, but the differences would seem so small as to indicate that only one taxon is involved.

Table 14 Size ranges of cnidae of *Anthopleura nigrescens* (in μm).

Location/ Type of cnida	Localities of specimens			
	Hawaii 'Holotype' (USNM 1925–1485)	Hawaii 'Paratype' (AMNH 1485)	Hawaii (present material)	
Tentacle				
Spirocyst	24·0–3·0	14·1–26·4 × 1·8–3·0	14·4–28·8 × 1·8–2·4	14·4–27·4 × 1·8–3·0
Basitrich	...	...	12·0–14·4 × 1·2	12·0–13·2 × 1·8
Basitrich	18·0–21·6 × 1·2–1·8	15·6–20·4 × 1·8–2·4	18·0–24·0 × 1·2–1·8	18·0–24·0 × 1·8
Column				
Basitrich	9·6–20·4 × 2·4–3·0	...	9·6–24·0 × 1·8–3·0	13·2–24·0 × 2·4–3·0
Heterotrich	...	...	16·8–24·0 × 3·0–4·0	19·2–21·6 × 3·6
Marginal spherule				
Spirocyst	26·4 × 2·4	...	...	...
Basitrich	9·6–13·2 × 1·8	12·0–20·4 × 1·8	9·6–13·2 × 1·2	8·4–19·2 × 1·8
Atrich	33·6–54·0 × 3·6–5·4	absent	33·6–54·0 × 3·6–5·4	43·2–54·0 × 3·6–4·8
Heterotrich	30·0–42·0 × 3·0–3·6	absent	31·2–42·0 × 3·0–3·6	30·0–42·0 × 3·0–3·6
Actinopharynx				
Basitrich	10·8–16·2 × 1·8	9·6–12·0 × 1·8	10·8–16·8 × 1·8	10·8–13·2 × 1·8
Basitrich	18·0–25·2 × 2·4–3·0	21·6–26·4 × 2·5–3·0	18·0–25·2 × 2·4–3·0	21·6–28·8 × 2·4–3·0
Microbasic amastigophore	19·0–20·0 × 3·6	19·2–24·0 × 3·0–3·6	19·2–20·4 × 3·6 (3 only)	19·2 × 3·6 (1 only)
Filament				
Basitrich	13·2–16·9 × 2·4	10·8–18·0 × 1·8	13·2–18·0 × 2·4	14·4–18·0 × 1·8
Basitrich	22·8–31·2 × 3·6–4·8	27·6–31·2 × 3·6–4·2	22·8–31·2 × 3·6–4·8	24·0–31·2 × 3·6–4·2
Microbasic p-mastigophore	...	...	14·4 × 2·4 (1 only)	9·6–15·6 × 2·4–3·0
Microbasic amastigophore	18·2–23·4 × 3·0–4·0	18·0–21·6 × 3·6	15·6–19·2 × 3·0–3·6	16·8–20·4 × 3·0–3·6

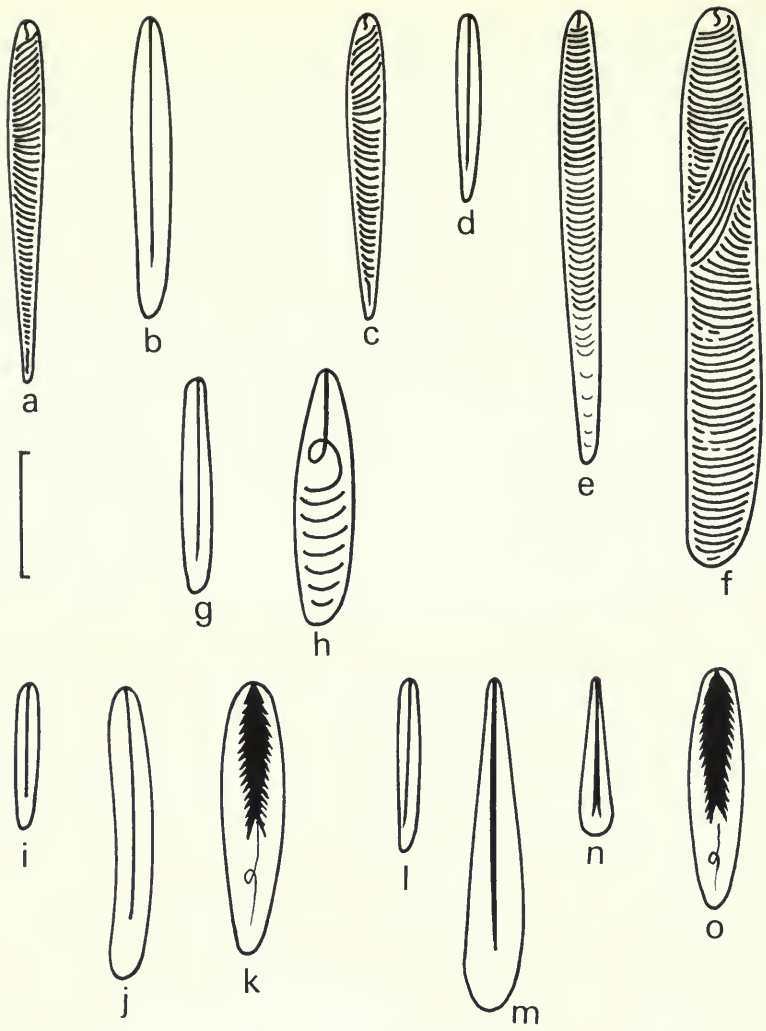

Fig. 23 *Anthopleura nigrescens*, nematocyst signature (see Table 14). *Tentacle* (a) spirocyst, (b) basitrich. *Marginal spherule* (c) spirocyst, (d) basitrich, (e) heterotrich, (f) atrich. *Column* (g) basitrich, (h) heterotrich. *Actinopharynx* (i-j) basitrichs, (k) microbasic amastigophore. *Filament* (l-m) basitrichs, (n) microbasic p-mastigophore, (o) microbasic amastigophore. Scale: (a-o) = 10 μm.

Anthopleura waridi (Carlgren, 1900), comb. nov.
Figs 24–26

Bunodes waridi Carlgren, 1900: 66–67, pl. 1 fig. 17.
Bunodactis waridi: Carlgren, 1949: 65; England 1969: 5.

Material Examined. Aden: Sapper Bay, 38 specimens, Sep 1966, BMNH 1983.8.4.87–106, 109–113. S. India: Mandapam Camp, 2 specimens, coll. C. E. Cutress, 15 Feb 1963, BMNH 1983.8.4.107–108.

Description. Column tall with vertical rows of adhesive verrucae, large in upper part of column becoming progressively smaller towards the limbus and extending to it. Each row of verrucae

terminating at margin in a large spherule on the parapet. Inside fosse a separate atrichal spherule on each primary endocoel and usually on 2nd and 3rd cycle endocoels, but sometimes irregularly arranged. Atrichal spherules small to large, tentaculoid, sometimes located close to but always separated from the marginal spherules (Figs 24a, d, e). Tentacles slender, tapered, arranged in three or more cycles. Disk flat. Base present. *Anatomy*. Sphincter strong, circumscribed (Fig. 24b).

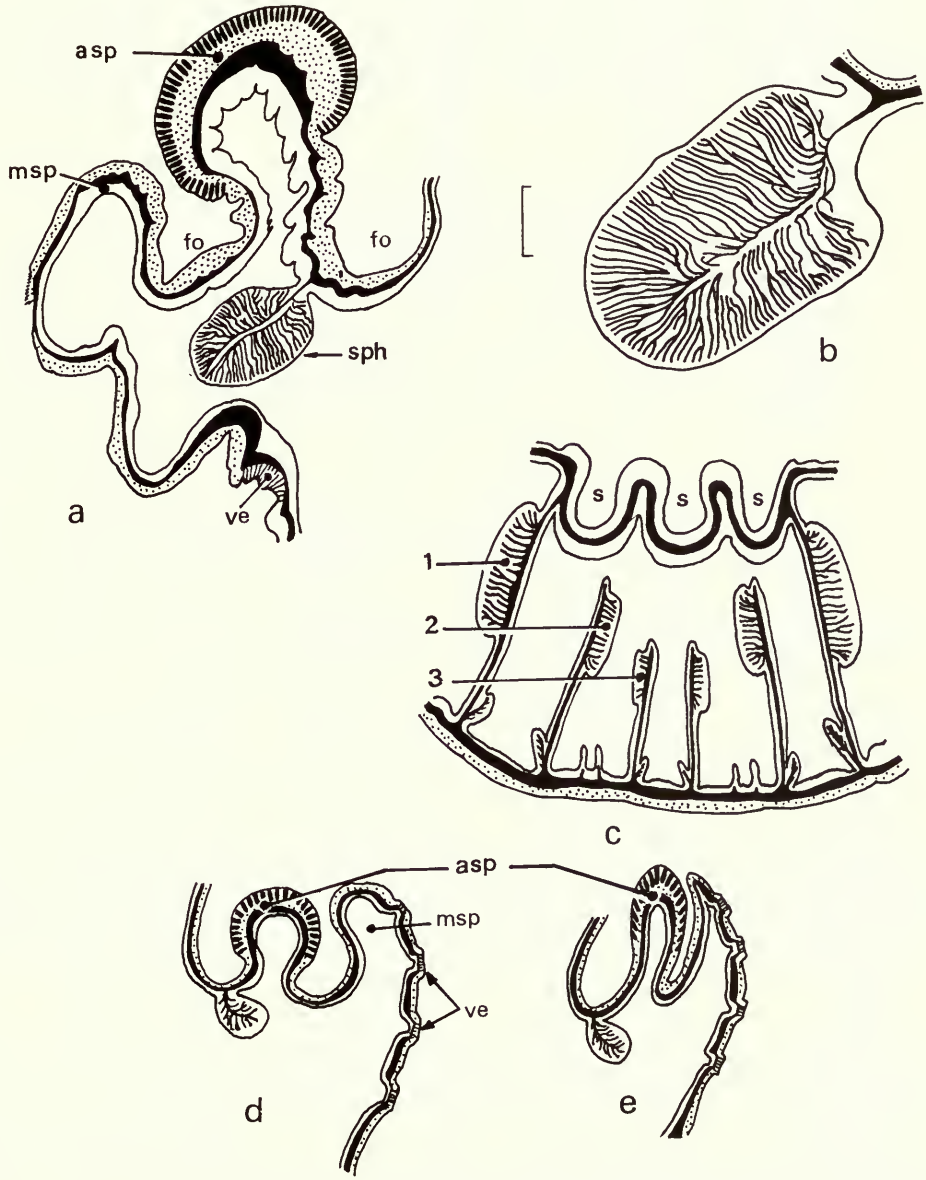

Fig. 24 *Anthopleura waridi*. (a) Vertical section of margin and sphincter with an atrichal spherule in the fosse, BMNH 1983.8.4.89. (b) Sphincter of (a) enlarged. (c) Development of triple pairs of directive mesenteries, in transverse section of column of same specimen. (d-e) Variation in shape of atrichal and marginal spherules in vertical sections of margin. Scale: (a) = 135 μm, (b) = 45 μm, (c-e) not to scale. (asp atrichal spherule, fo fosse, msp marginal spherule, s siphonoglyphs, sph sphincter, ve verruca, 1,2,3 are mesenteries of 1st, 2nd and 3rd pairs respectively. Stippled, ectoderm; black, mesogloea; white, endoderm.)

Mesenteries regularly or irregularly arranged, in up to four cycles; 1st and 2nd cycles perfect, 3rd cycle imperfect, 4th cycle only rudimentary, in some specimens not reaching disk. Siphonoglyphs 1–5, always supported by directives; sometimes in groups of three, with or without additional siphonoglyphs in other areas of actinopharynx. Mesentery development starting basally and proceeding upwards, resulting in a few more mesenteries at base than at top of column in some specimens; but in others number is same (Table 15). Retractor muscles strong, diffuse, on first cycle mesenteries, sometimes restricted. Parietobasilar muscles well developed, basilar muscles weak. Gonads on all older mesenteries including directives. Filaments absent from some younger cycles. Largest specimen, in contraction, height 13 mm, disk diameter 10 mm. *Cnidome*. See Table 16 and Figure 25. *Colour*. Column dull olive-green with bright or crimson verrucae; tentacles and disk translucent crimson.

Table 15 *Anthopleura waridi*. Relation between numbers of tentacles, mesenteries at disk and base, siphonoglyphs and spherules in four specimens (see BMNH 1983.87–106, 109–113).

	Mesenteries			
Tentacles	Disk	Base	Siphonoglyphs	Spherules
40	40	40	3	20
60	60	72	2	27
75	70	104	3	26
96	96	104	3	24

Table 16 Size ranges of cnidae of *Anthopleura waridi* (in μm).

Location/ Type of cnida	Specimens from Aden (BMNH 1983.8.4.84)	(BMNH 1983.8.4.85)	(BMNH 1983.8.4.86)
Tentacle			
Spirocyst	14·4–24·0 × 1·8–3·0	14·4–26·5 × 2·0–3·0	15·2–29·1 × 2·0–4·0
Basitrich	12·0–18·0 × 1·8–2·4	15·2–20·5 × 2·0–2·6	15·9–21·8 × 2·0–2·6
Column			
Basitrich	12·0–16·8 × 1·8–2·4	13·3–23·2 × 2·0–3·3	13·3–22·5 × 2·0–3·3
Heterotrich	18·0–21·6 × 3·0–3·6	15·2–29·5 × 4·6–6·0	20·0–26·5 × 5·3–6·0
Marginal spherule			
Spirocyst	13·3–36·3 × 2·0–4·0	17·2–33·0 × 2·0–3·3	23·2–37·0 × 3·3–4·0
Basitrich	12·0–16·8 × 2·0–2·4	11·3–15·2 × 2·0	12·0–20·4 × 2·0–2·4
Atrich	35·0–44·2 × 5·3–6·6	35·7–47·5 × 5·3–6·6	32·4–48·0 × 4·2–6·0
Heterotrich	32·4–41·0 × 4·6–5·3	29·8–44·2 × 4·0–5·3	32·4–44·4 × 3·6–4·8
Actinopharynx			
Basitrich	12·0–13·0 × 1·8	10·0–12·6 × 2·0–2·4	10·8–12·0 × 1·8
Basitrich	21·6–24·0 × 2·4	21·2–23·2 × 2·4–4·0	20·4–24·0 × 2·4
Microbasic amastigophore	18·0–20·4 × 4·2–4·8	18·5–21·2 × 4·0–4·6	18·0–24·0 × 4·8–5·4
Filament			
Basitrich	12·0 × 1·8	...	...
Basitrich	20·4–27·6 × 3·6–4·8	23·2–33·0 × 4·6–5·3	23·0–33·0 × 4·6–8·0
Microbasic p-mastigophore	12.0–14·4 × 2·4	16·6 × 3·3 (1 only)	...
Microbasic amastigophore	16·8–18·0 × 3·6–4·2	15·9–20·0 × 3·3–4·0	16·6–25·2 × 4·0–5·3

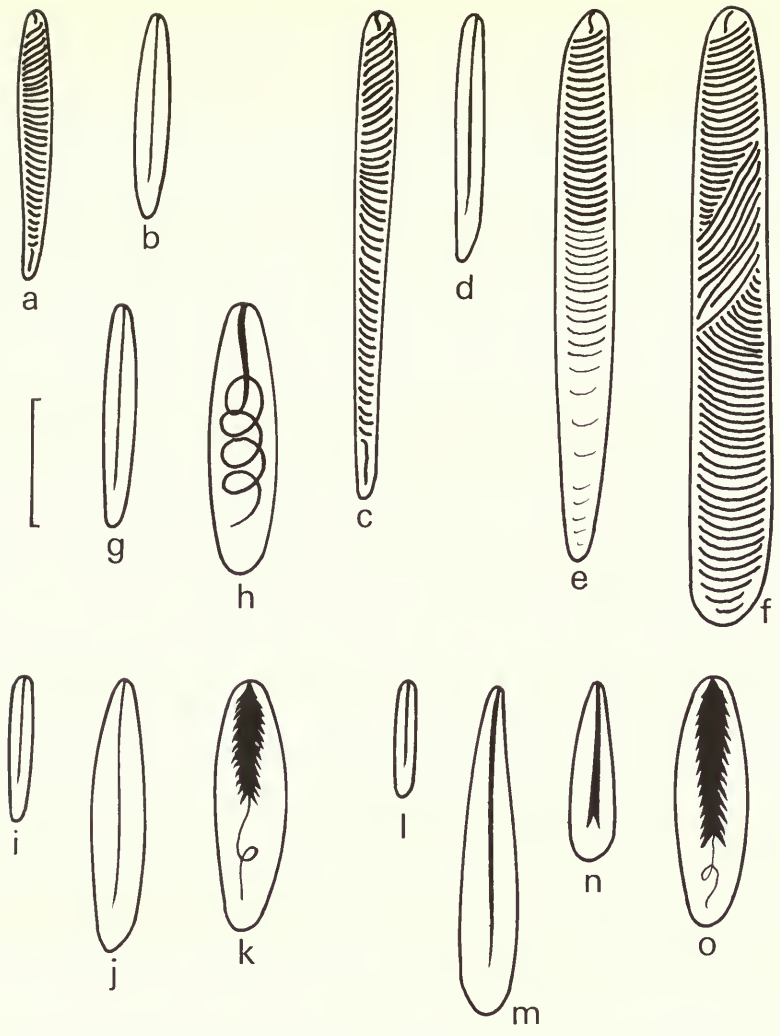

Fig. 25 *Anthopleura waridi*, nematocyst signature (see Table 16). *Tentacle* (a) spirocyst, (b) basitrich. *Spherule in the fosse* (c) spirocyst, (d) basitrich, (e) heterotrich, (f) atrich. *Column* (g) basitrich, (h) heterotrich. *Actinopharynx* (i-j) basitrichs, (k) microbasic amastigophore. *Filament* (l-m) basitrichs, (n) microbasic p-mastigophore, (o) microbasic amastigophore. Scale: (a-o) = 10 μm.

DISTRIBUTION. Zanzibar (Carlgren, 1900, as *Bunodes waridi*), Aden and S. India (present material).

HABITAT. Aden specimens found in old shells of rock oyster (*Crassostrea* sp.) and barnacles. Indian specimens on pieces of stone.

REMARKS. The verrucated column and atrichal spherules suggest that the material should be referred to *Anthopleura*. The presence of atrichal spherules in the fosse instead of on the parapet, and additional spherules on the parapet, indicate a different genus; but other characters of the species, especially the types of nematocyst, resemble those found in other species of *Anthopleura*. Also in some species of *Anthopleura* the nematocyst battery of a marginal spherule often forms a separate protuberance on the top or on the inner face (p. 210).

The colour in life recalls Carlgren's illustration of 1900 (pl. 1, fig. 17). Whilst colour of a species

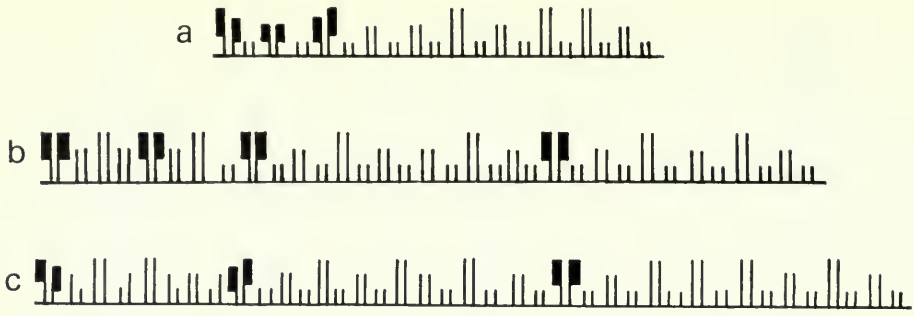

Fig. 26 *Anthopleura waridi*. Variation in arrangement of mesenteries in three specimens. (a) BMNH 1983.8.4.87, (b) BMNH 1983.8.4.88, (c) BMNH 1983.8.4.89. Directive mesenteries indicated by black rectangles.

is often of limited value in identification, in *A. waridi* it is distinctive and diagnostic. Carlgren stated that the species had forty-eight tentacles, twenty-four rows of verrucae and possessed 'pseudorandsackchen'. His illustration shows verrucae extending to the limbus. Carlgren (1949: 65) subsequently referred *A. waridi* to the genus *Bunodactis*. Examination of some poorly preserved specimens led me to identify them as *Bunodactis* (England, 1969: 5) (p. 209). Carlgren's description gives little additional information to assist in the identification since he did not describe the anatomy.

The only published description of a species of *Anthopleura* matching the particular mode of increasing the number of directive mesenteries and siphonoglyphs found in *A. waridi* is that of *A. dixoniana*. It appears that when a siphonoglyph is formed the area between the directives may develop further mesenteries. The two nearest the directives have their retractors facing outwards to complete two new pairs of directives: the next pair forms between the mesenteries of the second pair, possibly also to become directives (Fig. 24c). Additional pairs (non-directives) form between pairs of directives in the usual manner. Single siphonoglyphs meanwhile divide into two or three separate siphonoglyphs (Figs 24c and 26).

A. dixoniana differs from *A. waridi* in having atrichal spherules only on the margin and not also in the fosse; and in most of the 1st-cycle mesenteries being directives, which appear to arise in a different sequence. The sphincter of *A. dixoniana* is weak and varies in appearance while that of *A. waridi* is consistently strong-circumscribed. *A. nigrescens* (Verrill, 1928) also has several siphonoglyphs but they are never supported by directives as in *A. waridi*.

The remaining species of *Anthopleura* are not known to have atrichal spherules in the fosse or irregularly arranged mesenteries, and need not be considered further. The present material is, therefore, referred to *A. waridi* comb. nov.

Genus ***GYRACTIS*** Boveri, 1893

Gyractis Boveri, 1893: 241–253.

Actinioides Haddon & Shackleton, 1893: 126 (part); Haddon & Duerden, 1896: 1 (part); Haddon, 1898: 428 (part); Carlgren, 1900: 63; Carlgren, 1920: 151–153; Carlgren, 1938: 32.

Actiniogeton Carlgren, 1938: 32; Carlgren, 1949: 62; Carlgren, 1954: 579–580; Dunn, 1974*b*: 181–188.

DEFINITION. Actiniidae with well developed pedal disk. Column with longitudinal rows of adhesive verrucae. Marginal spherules large, often digitate, lacking atrichs. Sphincter weak, diffuse to circumscribed. Tentacles and mesenteries regularly or irregularly arranged. Siphonoglyphs two or more, which may or may not be connected to directive mesenteries. About same number of mesenteries distally as proximally. Retractor and parietobasilar muscles weak, diffuse; basilar

muscles present. Asexual reproduction by fission probably frequent. Cnidome: spirocysts, basitrichs and microbasic amastigophores.

TYPE SPECIES. *G. excavata* Boveri, 1893; by original designation.

REMARKS. Dunn, Fu-Shiang Chia & Levine (1980: 2078) have suggested that since *Aulactinia* (= *Bunodactis*) has been defined as being with or without marginal spherules (pseudospherules) some confusion might arise with the genus *Actiniogeton*, here regarded congeneric with *Gyractis*.

Aulactinia capitata Verrill, 1864, the type species of *Aulactinia*, lacks marginal spherules, as does *A. incubans* Dunn *et al.*, 1980. Other species originally referred to this genus [*B. reynaudi* (Milne Edwards, 1857), *B. mortenseni* (Carlgren, 1924), *B. maculosa* Carlgren, 1954, and *B.* (= *Epiactis*) *novazealandica* (Stephenson, 1918)] also lack marginal spherules (personal observation). Marginal cinclides are usually present, with consequent slight swelling of the margin between the mesenterial insertions, but spherules are absent (p. 210). Hence these species should not be placed in the same genus as one having prominent, often large, marginal spherules, as exist in *Gyractis excavata*. To resolve this problem it is suggested that *Aulactinia* be re-defined to include only species lacking marginal spherules. Species currently referred to *Aulactinia* (or *Bunodactis*) that have prominent marginal spherules should be transferred to *Gyractis*, the definition of which now accommodates both regularly and irregularly arranged species. The difference between regularly and irregularly arranged mesenteries is considered here to be a specific rather than a generic character.

Carlgren's (1938, 1949) definitions of *Actinioides* (= *Actiniogeton*), however, included only those species having irregularly arranged mesenteries. If this were the only difference between *Actiniogeton* and *Aulactinia*, then *Actiniogeton* could be considered congeneric with *Aulactinia*.

Dunn *et al.* (1980: 2077) discussed the presence of atrichs in the ectoderm of the outer tentacles of *Aulactinia incubans*. As they pointed out, those occur only sporadically and are about the same size as the basitrichs. It may be that such atrichs are partially discharged basitrichs in which the straight part of the thread has been discharged and then broken off. I have seen a similar artefact in species referred to other genera. It is possible that partial discharge occurs during killing and preservation, followed by the loss of the discharged portion by either chemical action or normal handling.

Gyractis excavata Boveri, 1893
Figs 27–28

Gyractis excavata Boveri, 1893: 250, pl. 10, figs 3–4, 6.
Gyractis pallida Boveri, 1893: 251, pl. 20, figs 1–2, 5.
Actinioides sesere Haddon & Shackleton, 1893: 126; Haddon, 1898: 428, pl. 22, figs 8–9, pl. 28, figs 1–2.
Actinioides sultana Carlgren, 1900: 63, pl. 1, figs 12–13; Carlgren, 1938: 33–35, figs 13–15.
Actinioides rapanuensis Carlgren, 1920: 151–153, figs 8–10.
Actiniogeton sesere: Carlgren, 1949: 62; Carlgren, 1954: 579–580, figs 9–11; Dunn, 1974*b*: 181–188, figs 1–6.
Actiniogeton rapanuensis: Carlgren, 1949: 62.
Actiniogeton sultana: Carlgren, 1949: 62.

MATERIAL EXAMINED Aden: 43 specimens, Oct 1966, BMNH 1983.8.24.1–10, 41–50; Maldives: Gan, Addu Atoll, 10 specimens, 8 Mar 1970, BMNH 1983.8.24. 11–20. Singapore: Pulau Biola, 29 specimens, 13 Sep 1970, BMNH 1983.8.24.21–40. Hawaii: 2 specimens, coll. D. F. Dunn, 1973. Torres Straits: Mabuaing, 4 specimens, coll. A. C. Haddon, Cambridge University Zoological Museum Co 177, type material of *Actinioides sesere* Haddon & Shackleton, 1893.

DESCRIPTION. Column short, verrucae in vertical rows, with debris and stones attached. Verrucae continuing onto large digitate marginal spherules, sometimes distorting them into frondose appearance. Verrucae small in clearly defined rows, or large irregularly arranged due to growth and distortion. Margin distinct. Fosse shallow, sometimes almost disappearing in full expansion. Disk wider than column, mouth sometimes raised on cone. Tentacles short, stout, tapered, in four or five circlets, occupying about one third of disk. Inner circlets in some specimens spaced away from third and succeeding ones. Pedal disk present. *Anatomy*. Siphonoglyphs 2–11. Directives absent. Mesenteries continuous from base to disk, arranged irregularly with at least 1st and 2nd

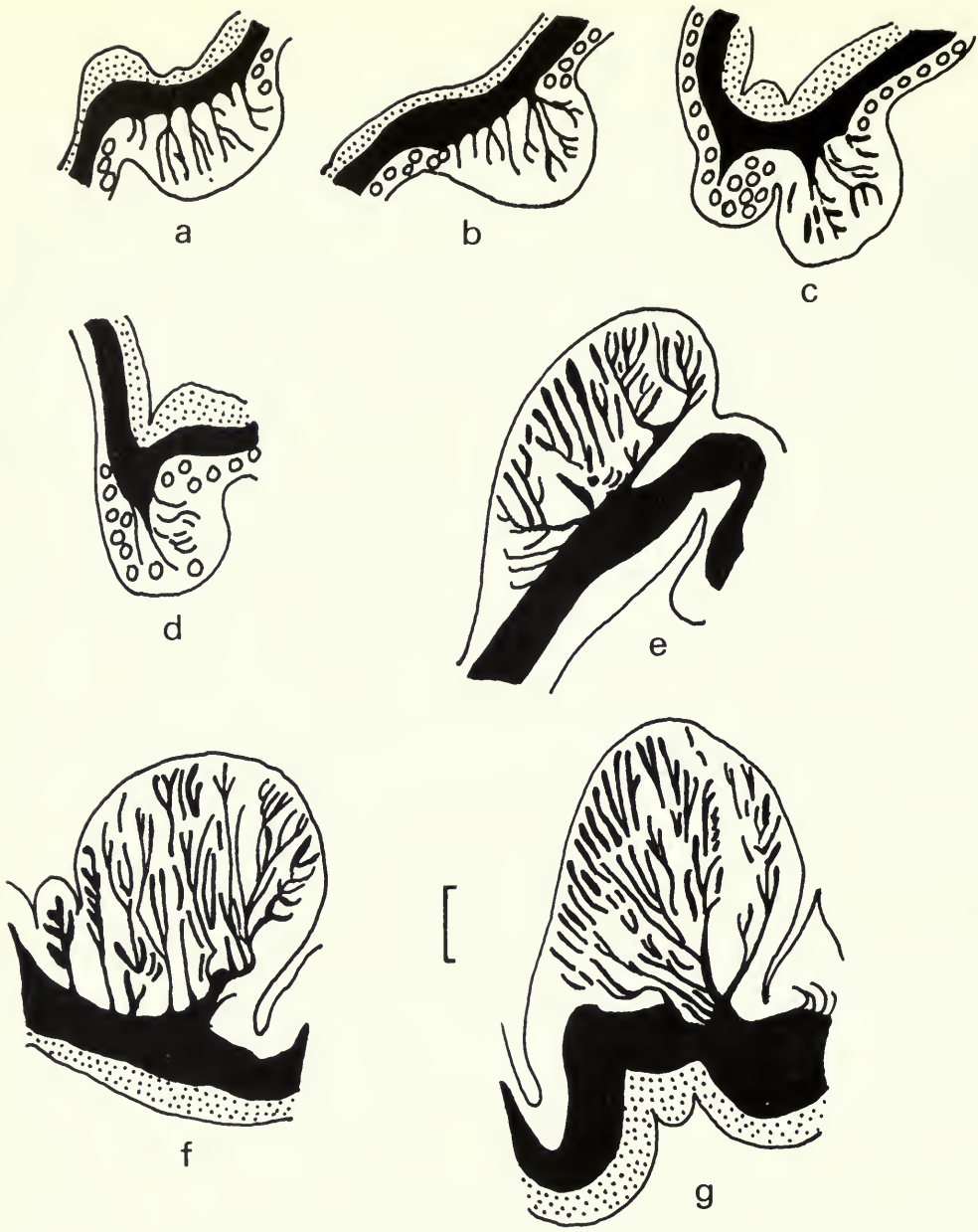

Fig. 27 *Gyractis excavata* Variation of sphincter muscle within and between specimens from different localities illustrated by vertical sections. (a-d) Aden, BMNH 1983.8.24.1–10. (e-g) Gan, BMNH 1983.8.24.11–20. (c-g) illustrate discontinuities noted in text (p. 258). Scale (a-d) = 25 μm, (e-g) = 50 μm. (Stippled, ectoderm; black, mesogloea; white, endoderm; circles, zooxanthellae.)

cycles perfect and usually a few of 3rd cycle; first three cycles fertile, 4th usually without filaments or gonads. Although gonads present, species habitually reproducing by fission, from base upwards. Retractor muscles diffuse to restricted-diffuse; parietobasilar muscles prominent, without free edge. Basilar muscles well developed (Dunn, 1974*c*). Sphincter muscle varied even within a single specimen, from weak-diffuse to weak-circumscribed (Fig. 27). Zooxanthellae present in

Table 17 Size ranges of cnidae of *Gyractis excavata* (in μm).

Location/ Type of cnida	Localities of specimens				
	Aden (BMNH 1983.8.24.1)	Aden (BMNH 1983.8.24.2)	Aden (BMNH 1983.8.24.3)	Gan (BMNH 1983.8.24.11)	Gan (BMNH 1983.8.24.12)
Tentacle					
Spirocyst	14·4–24·0 × 2·0–3·6	14·4–24·0 × 2·4–3·0	13·0–21·5 × 2·4–3·0	14·4–26·4 × 2·4–3·0	15·6–25·2 × 2·4–3·6
Basitrich	12·0–18·0 × 2·4–3·0	12·0–19·2 × 2·4–3·0	12·0–20·2 × 2·0–3·0	14·1–19·5 × 2·4–3·0	12·0–21·6 × 2·4–3·0
Column					
Basitrich	15·6–18·0 × 2·0–2·4	13·2–18·0 × 2·0	8·5–17·6 × 2·4	8·5–18·0 × 2·0–2·4	12·0–19·2 × 2·0–2·4
Actinopharynx					
Basitrich	...	...	9·8–13·0 × 2·0	...	...
Basitrich	16·8–22·8 × 2·4–3·0	19·2–24·0 × 3·6	18·2–24·7 × 2·6	18·2–24·1 × 2·4–3·6	18·0–28·8 × 2·4–3·6
Microbasic amastigophore	21·6–26·4 × 4·2	22·8–26·4 × 3·6–4·2	20·8–22·8 × 4·0–4·6	20·8–24·7 × 4·6–5·2	16·9–22·8 × 4·0–4·6
Filament					
Basitrich	10·8–16·8 × 2·4	10·8–16·8 × 2·0–2·4	9·8–18·0 × 2·0	9·8–14·3 × 2·0	10·4–14·4 × 2·0
Basitrich	21·4–32·4 × 2·4–4·2	22·8–32·4 × 3·0–3·6	20·8–32·4 × 2·6–3·3	26·0–32·4 × 3·3–4·0	28·8–34·8 × 3·6–4·8
Microbasic p-mastigophore	12·0–14·4 × 2·4	13·2–14·4 × 2·4–3·0	13·0–15·0 × 2·4	18·3 × 2·4 (2 only)	13·2–15·6 × 3·6–4·2
Microbasic amastigophore	18·0–25·2 × 3·6–4·8	19·2–22·8 × 3·6–4·2	19·5–22·8 × 4·0–4·6	18·2–26·0 × 4·0–4·6	20·8–26·4 × 3·6–4·2

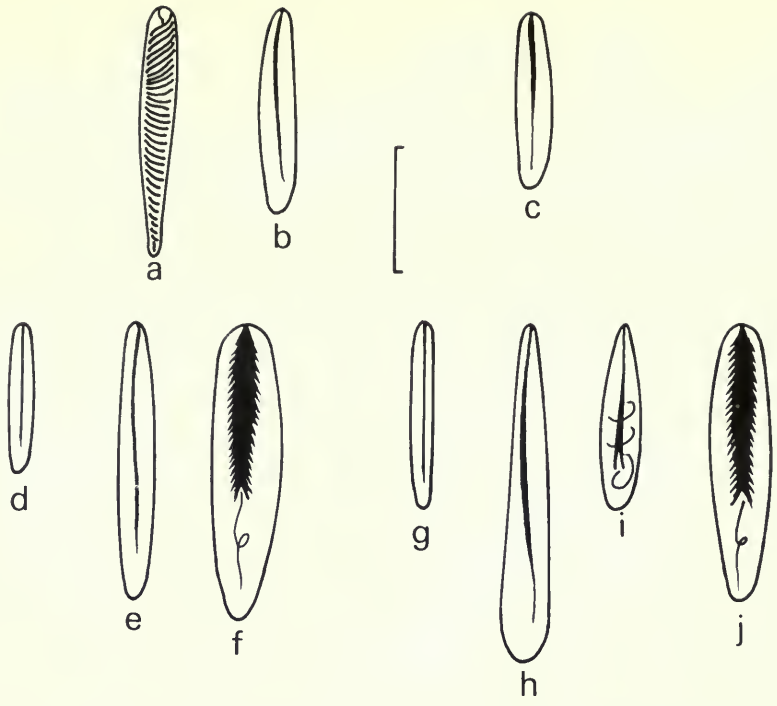

Fig. 28 *Gyractis excavata*, nemotocyst signature (see Table 17). *Tentacle* (a) spirocyst, (b) basitrich. *Column* (c) basitrich. *Actinopharynx* (d-e) basitrichs, (f) microbasic amastigophore. *Filament* (g-h) basitrichs, (i) microbasic p-mastigophore, (j) microbasic amastigophore. Scale: (a-j) = 10 μm.

endoderm of tentacles, disk, upper column and filaments. *Cnidome*. See Table 17 and Figure 28. Basitrichs of spherules of same size range as those of column. Microbasic amastigophores of actinopharynx scarce. *Colour*. Column flesh at base grading upwards through green to grey near margin. Verrucae bright green or pink. Disk and tentacles of three colour morphs: (a) disk grey, tentacles brown with white subterminal band; (b) disk green, tentacles brownish, lacking subterminal band; (c) disk and tentacles patterned green with irregular pink markings.

Distribution. Reported from Torres Strait (Haddon & Shackleton, 1893, as *Actinioides sesere*), Sri Lanka (Boveri, 1893), Zanzibar and Durban (Carlgren, 1900, 1938, as *Actinioides sultana*), W Australia (Carlgren, 1954, as *Actiniogeton sesere*), Hawaii (Dunn, 1974*b* as *Actiniogeton sesere*), Aden, Gan and Singapore (present material) and Fiji (J. S. Ryland, pers. comm., det. D. Fautin).

Habitat. Numerous in rock crevices on exposed outer edges of reefs, and many carpet large areas. At the Aden and Gan localities many specimens packed tightly together into cracks in a red granite or basalt. In Singapore on dead coral.

Remarks. The specimens from Aden and Gan seemed to be of two species. Those from Aden, while having the same coloration and general form as those from Gan and occupying a similar habitat, were more delicate. The verrucae of the Aden population were smaller and arranged in vertical rows. The spherules too were smaller and not distorted by verrucae; and the sphincters were much weaker (Fig. 27). On the other hand the sphincter was of the same pattern throughout and the apparent interpopulation differences could be found in a single specimen. The muscle folds of the sphincters from both localities were often discontinuous (Fig. 27c-g), but this was not considered an artefact. All specimens of the samples examined had several siphonoglyphs without directive

Table 18 Comparison of cnidae size ranges of certain conspecific species of *Gyractis* (in μm).

Location/ Type of cnida	*Actinioides sesere* (Cambridge Univ. Zool. Mus. Coll. A.C. Haddon)	*Actiniogeton sultana* (Carlgren 1938)	*Actiniogeton sesere* (Carlgren 1954)	*Actiniogeton sesere* Hawaii. Coll. D. F. Dunn	*Actiniogeton rapanuensis* (Carlgren 1920)
Tentacle					
Spirocyst	14·4–19·2 × 1·8–2·4	11·0–22·0 × 1·5–2·5	...	10·4–19·5 × 2·0	12·0–26·0 × 1·0–2·5
Basitrich	12·0–24·0 × 1·8–3·0	14·0–18·0 × 2·0–2·5	12·7–17·0 × 2·5–2·8	13·0–26·0 × 2·6–4·0	16·0–19·0 × 2·0
Column					
Basitrich	8·4–16·8 × 1·2–2·4	14·0–17·0 × 2·0–2·5	14·0–17·0 × 2·8	9·8–19·5 × 2·0	13·0–17·0 × 2·8
Actinopharynx					
Basitrich	19·2–24·0 × 2·4	21·0–24·0 × 3·0–3·5	17·0–24·0 × 3·5	18·2–29·3 × 2·6–3·3	17·0–24·0 × 2·5
Microbasic amastigophore	22·8–4·6 (1 only)	21·0–24·0 × 5·0	19·7–21·0 × 5·0–6·0	20·8–28·4 × 4·6–5·9	...
Filament					
Basitrich	10·8–15·6 × 2·0	...	14·8–18·3 × 2·0	9·5–13·0 × 2·0	...
Basitrich	24·0–31·2 × 2·4–3·6	28·0–31·0 × 3·0–3·5	25·0–28·0 × 4·2	26·0–33·6 × 2·6–4·0	...
Microbasic p-mastigophore	12·0–14·4 × 2·4–3·6	...	...	14·3–16·3 × 2·6	...
Microbasic amastigophores	15·6–25·2 × 3·0–4·8	19·0–24·0 × 4·5–5·0	25·0–28·0 × 4·2	19·5–26·0 × 4·0–5·2	...

Note: The data from Haddon's and Dunn's material were obtained by myself. Haddon did not give data on nematocysts; and my findings in respect of Dunn's material differ slightly from those previously published (Dunn, 1974*b*; see p. 186).

mesenteries, and the size ranges and types of cnidae present were identical. The specimens from Singapore had the same variations as those from Aden and Gan.

Boveri (1893: 250–252) described two species of sea-anemone which differed only in the type of sphincter, and because they were not bilaterally symmetrical he proposed a new family, the Holoactiniidae, to include them. He proposed the genus *Gyractis* to accommodate the two species and named them *G. excavata* and *G. pallida*. His definition of *Gyractis* included a verrucated column and digitate marginal spherules, and the tentacles were said to occupy approximately half of the area of the disk with a clear gap between the 2nd and 3rd cycles. According to Boveri's description these two species lacked directive mesenteries, as the pairs of retractor muscles always faced each other: hence the absence of bilateral symmetry. He stated that there were no siphonoglyphs but if each were little differentiated from the rest of the actinopharynx there might nevertheless have been many. Boveri's illustrations of both species (1893, pl. 10, figs 1–6) show the whole animal, the arrangement of the tentacles and of the sphincter muscles, which together with the absence of directive mesenteries conform to the description given here. The colour varieties described by Boveri encompass those recorded above. The present material is thus referred solely to *Gyractis excavata* Boveri, 1893, the first of his two species. The second species, *G. pallida*, is here considered conspecific with *G. excavata*, since it has been shown that the sphincter can vary within a single specimen (Fig. 27). Under the first reviser principle the name *excavata* is given priority over *pallida*.

Though the description of *Actinioides sesere* (Haddon, 1898: 428) was incomplete the verrucated column, the capitulum provided with well defined conical acrorhagi, and the absence of gonadial grooves, show that the species is similar to *G. excavata*. Examination of four of Haddon's specimens held at Cambridge University Zoological Museum (by kind permission of the curator Dr C. B. Goodhart) confirmed that the species was identical with that of Boveri. There were no directive mesenteries but there were many siphonoglyphs, 7, 8, 9 and 9 being recorded. The types and size ranges of the cnidae taken from one of the specimens were close to those found in the present material (Table 18). *Actinioides sesere* is thus considered conspecific.

Actinioides sultana Carlgren, 1900: 63, was based on material from Zanzibar, and later redescribed (Carlgren, 1938: 33) from material collected from Durban. Carlgren's illustrations (1938, fig. 13) and description, including the size ranges of cnidae (Table 18), conform to the range of *G. excavata* given here. The coloration described by Carlgren resembles closely that which I have seen. Also, the sites at Aden and Gan were identical to that described by Carlgren (1938: 34) as 'low water, numerous specimens, congregated closely together and forming carpets on flat rocks'. Thus *A. sultana* is also considered conspecific with *G. excavata*.

Carlgren (1938: 23) also commented on the genus *Actinioides* Haddon & Shackleton, 1893, which Stephenson (1922: 271) had supposed was congeneric with *Bunodactis*. Carlgren pointed out that if *Actinioides dixoniana*, the type species of the genus *Actinioides*, were shown to have acrorhagi proper (that is, with atrichs), and if there were more mesenteries at the base than at the margin, then the genus *Actinioides* would indeed lapse. Since the species *A. sultana* (Carlgren, 1938: 33) certainly belonged neither to *Bunodactis* nor to *Anthopleura*, Carlgren said a new genus was required and he proposed *Actiniogeton* (Carlgren, 1938: 32). It has been shown that *Actinioides dixoniana* is best referred to *Anthopleura* (p. 240–245), and *Actiniogeton* might thus become a valid genus. However, for the reasons stated (p. 255) *Actiniogeton* is here considered to be congeneric with *Gyractis*.

Actinioides rapanuensis Carlgren, 1920: 151, was said to lack siphonoglyphs and directives. Its sphincter varies as in *G. excavata* and the size ranges of the cnidae reported resemble those of the present material (Table 18). It is thus considered that siphonoglyphs are probably present, although the species was first thought to lack them as were *A. sesere* and *A. sultana*. Thus *A. rapanuensis* is regarded conspecific with *G. excavata*.

Actiniogeton sesere (Dunn, 1974*b*: 181–188), based on material from Hawaii, has all the characters but one of *G. excavata*. The exception, recorded by Dunn, was a single atypical structure having the appearance of siphonoglyph. But in two specimens she kindly lent me 3 and 5 siphonoglyphs were found. In her description the presence of microbasic p-mastigophores in the

column ectoderm is mentioned. The present specimens from Gan seemed to lack them, but in some specimens from Aden occasional microbasic amastigophores were seen. The ratio of microbasic amastigophores to basitrichs was 1 : 466 (4 amastigophores, 1860 basitrichs and 2 spirocysts). In one of Dunn's specimens 1035 basitrichs were counted but no amastigophores and it seems possible that in Dunn's paper the types and size ranges of the cnidae in the column and in the actinopharynx were inadvertently transposed.

Revised data on type and size range of cnidae from one of Dunn's specimens are given in Table 18. *A. sesere* sensu Dunn, 1974*b*, is also considered conspecific with *G. excavata*.

Carlgren (1947: 14–15) examined some specimens which he believed to have been studied by Boveri. In a personal communication to Carlgren, Boveri stated that he had placed specimens of both *G. excavata* and *G. pallida* in a jar without a label. Carlgren found artrichal marginal spherules in the specimens and he thought they were *Gyractis*. He concluded that *Gyractis* was congeneric with *Anthopleura*. Carlgren also stated that several other specimens in small jars from a Dr Ondaajte's collection, the source of Boveri's material, similarly had atrichal marginal spherules; and some of these specimens were accompanied by figures showing a rich variety of colour. Several species of *Anthopleura* which occur in the Indian Ocean have bright colours but the only one likely to be confused anatomically with *Gyractis* is *A. nigrescens*. It too has several siphonoglyphs and no directive mesenteries (p. 248–250) but it can be distinguished from *Gyractis* by its prominent atrichal spherules with conspicuous nematocyst batteries, and in contrast its colour is usually dull brown to black. From Carlgren's remarks there seems no evidence to connect the specimens he examined with Boveri's *Gyractis* material, and in view of Boveri's excellent description it is doubtful that Carlgren's specimens were *Gyractis*.

Of the four remaining species originally referred to *Actiniogeton* Carlgren, 1949, *A. papuensis* Haddon, 1898: 426, is conspecific with *Anthopleura dixoniana* (p. 240–245). From the original description *Actinioides spenceri* Haddon & Duerden, 1896: 159, is unlikely to be referrable to *Gyractis*, since it is reported as having more mesenteries at the base than at the margin and possibly atrichal marginal spherules. However, when Carlgren (1938: 33) examined Haddon & Duerden's slides of *A. spenceri* he could not detect the presence of atrichs though he reported spherules to be present.

Actinioides ambonensis Kwietniewski, 1897: 389, needs to be re-examined before a decision can be made: it was described as having regularly arranged mesenteries, two siphonoglyphs and 24 conical spherules but Carlgren (1938: 33) was doubtful of these details.

Genus *MESACTINIA* nov.

Definition. Actiniidae with wide pedal disk. Column smooth, short, with scapus and capitulum. Margin with prominent perforate spherules, with one or more small suckers on the outer surface. Siphonoglyphs varied in number. Mesenteries regularly or irregularly arranged, with or without directives; growing from disk downwards, but same number distally as proximally. Some mesenteries of last cycle weak near base.

Many perfect mesenteries; at least 1st and 2nd cycle fertile. Sphincter diffuse-weak. Asexual reproduction common. Retractor muscles diffuse, parietobasilar and basilar muscles well defined. Cnidome: spirocysts, basitrichs, microbasic amastigophores and microbasic p-mastigophores.

Type Species. *Mesactinia ganensis* gen. nov., sp. nov., by monotypy.

Remarks. A new genus is proposed to include a species of actiniid having the above characters. Carlgren (1949) listed only two genera having spherules (pseudospherules) and having the same number of mesenteries distally and proximally: *Tealianthus* Carlgren, 1927: 38, had the 1st cycle sterile, and *Isotealia* Carlgren, 1898: 25, had the first two cycles sterile. The species which *Mesactinia* is proposed to accommodate has the 1st and 2nd cycles fertile and thus differs from species usually referred to either of the other genera. Although the type species of *Mesactinia* usually shows an irregular arrangement due to asexual reproduction, the definition allows for the presence of species with regular arrangements of mesenteries and tentacles.

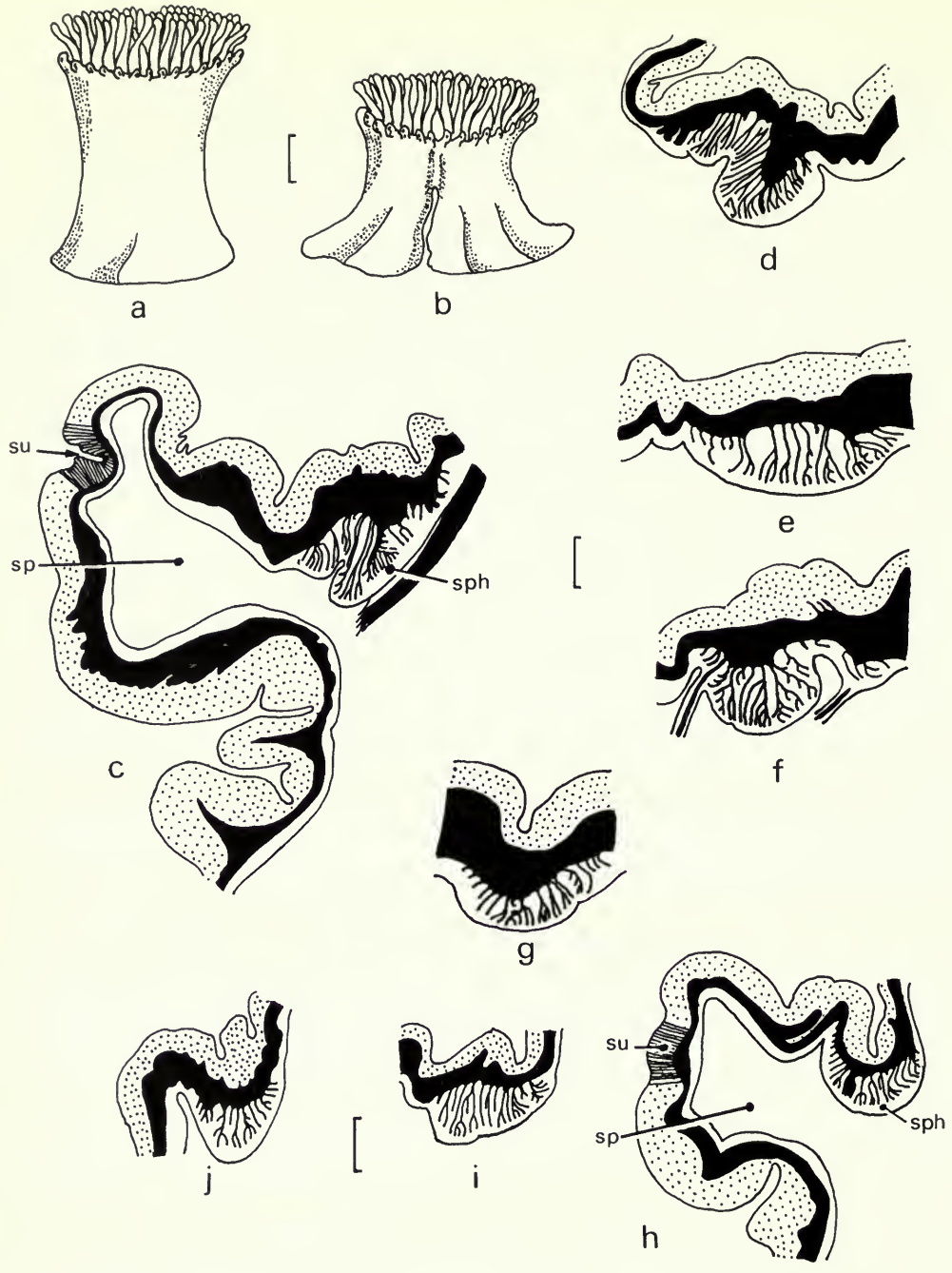

Fig. 29 *Mesactinia ganensis* gen. nov., sp. nov. (a) General appearance. (b) A specimen dividing into two from the base. (c) Vertical section of margin, BMNH 1984.2.9.90. (d-g) Variation in sphincter muscle in vertical sections of BMNH 1984.2.9.111–119. (h) Vertical section of margin of specimen from Singapore, BMNH 1984.2.9.83. (i-j) Vertical section showing variation in sphincter between two specimens from Singapore. Scale: (a-b) = 4 mm, (d-j) = 90 μm. (sp marginal spherule, sph sphincter, su sucker. Stippled, ectoderm; black, mesogloea; white, endoderm.)

Mesactinia ganensis gen. nov., sp. nov.
Figs 29–30

TYPE LOCALITY AND MATERIAL. Holotype: Gan Island, Addu Atoll, Maldives, 10 Feb 1970, BMNH 1984.2.9.90. Paratypes: Gan Island, 10 specimens, 10 Feb 1970, BMNH 1984.2.9.2–8; c. 50 specimens, 7 Mar 1970, BMNH 1984.2.9.10–69. Singapore: Pulau Biola, 20 specimens, 13 Sep 1970, BMNH 1984.2.9.88–110; Pungol Point, 10 specimens, 11 Feb 1971, BMNH 1984.2.9.111–119. Malaysia: Pulau Tioman, 25 specimens, BMNH 1984.2.9.120–145.

DESCRIPTION. Column slightly taller than wide or about equal in height and diameter, smooth with regularly or irregularly arranged large perforate marginal spherules on clearly defined parapet (Fig. 29a, b). Spherules with one or two small suckers on outer surface (Fig. 29c, h). Fosse shallow, capitulum distinct. Tentacles up to two hundred, long, slender, with rounded tips which are often dilated in life, but not capitate since special types or concentrations of nematocysts absent; in several cycles, inner about half way between mouth and margin, a clear gap between this cycle and next outer one. Oral disk wider than column, sometimes lobed; when contracted forming long funnel into body. Frequently reproducing by longitudinal fission, commencing at pedal disk (Fig. 29b). *Anatomy*. Mesenteries irregularly arranged, in four to five cycles, without directives. Sometimes one mesentery of a pair smaller than the other. Siphonoglyphs up to five, small to almost inconspicuous, or prominent. About same number of mesenteries distally as proximally, occasionally a few more distally since they grow from margin to base (p. 214). Near base mesenteries of last cycle extremely small and only visible as line on column wall, but apparent in sections. At least older mesenteries perfect and fertile, later cycles lacking filaments. Retractor muscles present. Oral and marginal stomata present. Sphincter varied, weak-diffuse (Figs 29d-i).

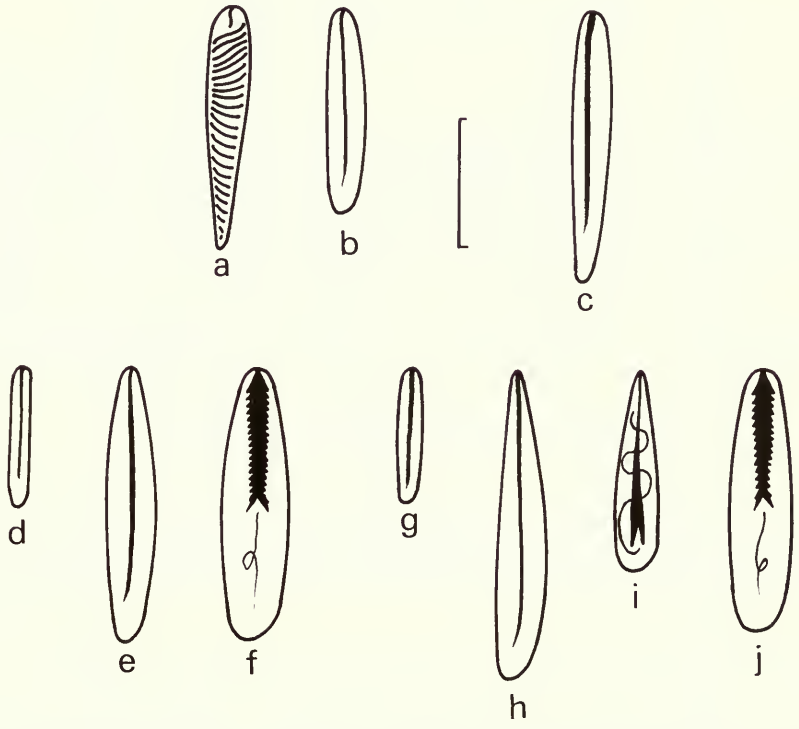

Fig. 30 *Mesactinia ganensis* gen. nov., sp. nov., nematocyst signature (see Table 19). *Tentacle* (a) spirocyst, (b) basitrich. *Column* (c) basitrich. *Actinopharynx* (d-e) basitrichs, (f) microbasic amastigophore. *Filament* (g-h) basitrichs, (i) microbasic p-mastigophore, (j) microbasic amastigophore. Scale: (a-j) = 10 μm.

Table 19 Size ranges of cnidae of *Mesactinia ganensis* gen. nov., sp. nov. (in μm).

Location/ Type of cnida	Localities of specimens				
	Gan-Addu Atoll 'Holotype'	Pulau Biola (BMNH 1984.2.9.88)	Pungol Point (BMNH 1984.2.9.111)	Pungol Point (BMNH 1984.2.9.112)	Pungol Point (BMNH 1984.2.9.113)
Tentacle					
Spirocyst	13·3–22·5 × 2·6–4·0	14·0–21·2 × 2·6–4·0	15·9–25·2 × 2·6–4·0	13·3–23·8 × 2·0–3·3	16·5–23·6 × 2·0–2·4
Basitrich	15·2–20·0 × 2·0–2·6	13·3–18·5 × 2·6–3·3	15·9–20·0 × 2·6	14·0–21·2 × 2·6–3·3	15·3–20·0 × 2·4–3·3
Column					
Basitrich	20·0–28·5 × 2·6	17·9–23·2 × 2·6	18·5–26·5 × 2·6	20·5–25·8 × 2·6	14·2–23·6 × 2·4–3·0
Actinopharynx					
Basitrich	9·3–10·0 × 2·0	...	10·6 × 2·0	...	8·2–10·6 × 2·0
Basitrich	19·2–24·5 × 3·3–4·0	18·5–22·5 × 3·3	17·9–24·5 × 3·3–4·0	19·2–24·5 × 2·6–4·0	14·2–23·6 × 2·4–2·0
Microbasic amastigophone	20·5–24·5 × 3·3–4·0	20·5–23·2 × 4·6–5·3	23·2–25·2 × 5·3	23·2–25·2 × 4·6–5·3	20·0–23·6 × 3·3–4·6
Filament					
Basitrich	10·0–10·6 × 2·0	10·0–11·3 × 2·0	10·0–10·6 × 2·0	10·6–11·0 × 2·0	8·2–9·4 × 2·0
Basitrich	25·2–29·8 × 3·3–4·0	24·5–31·7 × 3·3–4·0	25·2–28·5 × 4·0	24·5–29·8 × 3·3–4·6	17·7–29·5 × 2·6–3·3
Microbasic p-mastigophore	16·6–21·8 × 2·6–3·3	15·9–23·8 × 3·3–4·0	13·3–21·8 × 3·3–4·0	14·0–20·0 × 3·3–4·0	13·0–20·0 × 3·0–3·5
Microbasic amastigophore	19·2–24·5 × 3·3–4·6	18·5–23·2 × 3·3–4·6	21·2–24·5 × 3·3–4·6	17·9–24·5 × 3·3–4·6	18·9–22·4 × 3·5

Circular muscle folds of column low, comprising mostly unbranched single folds. Marginal spherules on most endocoels, and in adult specimens on some exocoels. Zooxanthellae present in endoderm of tentacles, disk and upper column. *Cnidome*. See Table 19 and Figure 30. Marginal spherules with basitrichs of same size range and type as column. *Colour*. Column rosy pink grading to green towards margin. Tentacles brown with faint blue sheen, sometimes with white bar near base. Disk brown, mouth flesh tone. Spherules brown with white tips. Occasional specimens had column yellowish grading to green near margin, with disk brown tinged green, and spherules brown with bright green tips.

DISTRIBUTION. Recorded from the Maldives, Singapore, and Pulau Tioman on the east coast of Malaysia (type series).

HABITAT. Specimens from Gan on dead stags-horn coral (*Acropora* sp.), many specimens on each branch, about 1 m below MLTL, near reef edge. Similar habitat in Singapore but also on stones in mud above MLTL. Associated with the population at Pulau Tioman was *Antheopsis malayensis* sp. nov. (p. 274).

REMARKS. Some of the characters of the present species are similar to those of *Telactinia citrina* comb. nov. (p. 269), especially the large marginal spherules and the nematocyst signature. *T. citrina*, however, is separated as having more mesenteries at the margin that at the base, the youngest cycles ending abruptly near the margin; whereas the present species has about the same number of mesenteries throughout the column. Further, the number of siphonoglyphs in *Mesactinia ganensis* gen. nov., sp. nov. varies up to a maximum of five and they are never supported by directives. Hence *M. ganensis* cannot be accommodated in *Telactinia* as defined here. The species is, therefore, referred to a new genus *Mesactinia* nov.

Genus ***NEOCONDYLACTIS*** nov.

? *Paracondylactis* Carlgren, 1934: 28 (part).

DEFINITION. Actiniidae with elongate column having verrucae in upper part, lower column being smooth. Margin distinct with marginal spherules. Sphincter diffuse to restricted-diffuse, weak. Tentacles simple, hexamerously arranged. Two siphonoglyphs supported by directives. Same number of mesenteries distally and proximally, all or almost all perfect; all fertile including directives. Retractors diffuse. Cnidome: spirocysts, basitrichs and microbasic amastigophores.

TYPE SPECIES. *Neocondylactis singaporensis* gen. nov., sp. nov., by monotypy.

REMARKS. A new genus is required to cover species having the characters defined above. Figure 31 shows the characters of *Neocondylactis* gen. nov. and related genera.

Neocondylactis singaporensis gen. nov., sp. nov.
Figs 32–33

? *Paracondylactis hertwigi*: Carlgren, 1934: 28.

TYPE LOCALITY AND MATERIAL. Holotype: Singapore: Pungol Point, 19 May 1970, BMNH 1983.11.81.1. Paratypes: Pungol Point, 9 specimens, 19 May 1970, BMNH 1983.11.18.7–15; 3 specimens, Feb 1971, BMNH 1983.11.18.16–19; Pasir Ris, 6 specimens, 24 Mar 1970, BMNH 1983.11.18.2–6.

DESCRIPTION. Column elongate, trumpet shaped, disk much wider than base; hour-glass shaped in contraction. Upper part of column with twenty-four vertical rows of endocoelic verrucae, up to six per row. Margin with large spherules, some of which may be compound (Fig. 32a). Often small additional exocoelic spherules in older specimens. Sometimes verrucae on outer face of spherules. Lower part of column smooth. Tentacles long, slender, tapering to rounded tip, up to 48. Disk flat, mouth with two siphonoglyphs. Base adherent. Height 25 mm contracted, extending up to 75 mm; diameter contracted 15 mm widening to 20 mm. *Anatomy*. Mesenteries arranged hexamerously, in

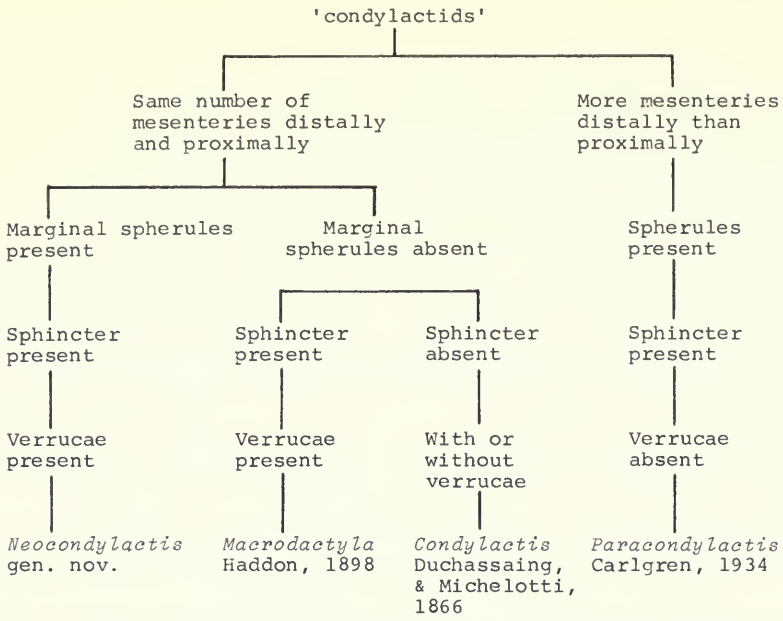

Fig. 31 Key to genera *Neocondylactis* gen. nov., *Macrodactyla, Condylactis* and *Paracondylactis.*

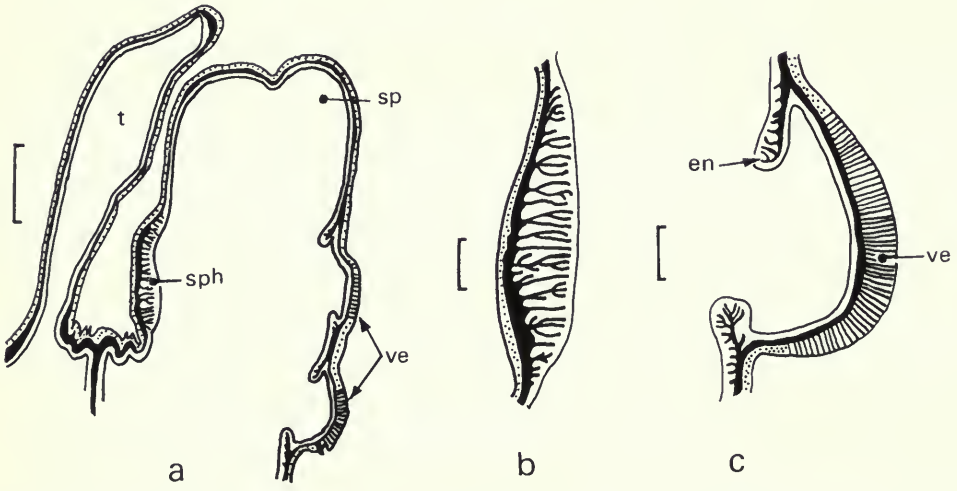

Fig. 32 *Neocondylactis singaporensis* gen. nov., sp. nov. (a) Vertical section through margin. (b) Vertical section through sphincter muscle. (c) Vertical section through a verruca, illustrating apparent sphincters consisting of thickened circular muscle. Scale: (a) = 200 μm, (b-c) = 50 μm. (en endodermal circular muscle, sp spherule, sph sphincter, t tentacle, ve verruca. Stippled, ectoderm; black, mesogloea; white, endoderm.)

three cycles, 6—6—12 pairs; all or almost all perfect, 1st cycle attached along whole length of actinopharynx, 2nd cycle along upper half and 3rd cycle attached along distal quarter only. Same number of mesenteries at margin as at base. Filaments not extending to base, occupying only two thirds of length of mesentery. Gonads located in upper part of mesentery only. All mesenteries fertile, including directives. Siphonoglyphs prolonged aborally with extension of actinopharyx on

Table 20 Size ranges of cnidae of *Neocondylactis singaporensis* gen. nov., sp. nov. (in μm).

Location/ Type of cnida	Localities of specimens		
	Pungol Point 'Holotype'	Pasir Ris (BMNH 1983.11.18.2)	Pungol Point (BMNH 1983.11.18.7)
Tentacle			
Spirocyst	11·7–22·8 × 2·0–2·6	9·9–23·2 × 1·3–2·6	15·9–23·2 × 2·6–3·3
Basitrich	16·3–21·5 × 2·0–2·6	15·9–19·9 × 2·0–2·6	13·3–16·6 × 2·0
Column			
Basitrich	9·1–16·3 × 2·0	7·9–16·6 × 1·3–2·0	9·3–16·6 × 2·0–2·6
Actinopharynx			
Basitrich	18·9–29·3 × 2·6–3·3	16·6–22·5 × 2·0–2·6	23·2–26·5 × 2·6–4·0
Microbasic amastigophore	15·6–20·8 × 4·0–4·6	15·9–18·5 × 3·3–4·6	17·2–21·1 × 4·0
Filament			
Basitrich	10·4–11·7 × 1·3	9·9–17·2 × 1·3	9·8–11·1 × 1·3–2·0
Basitrich	26·0–33·2 × 4·0–4·6	23·2–28·7 × 3·3–4·2	28·0–35·8 × 4·0–4·6
Microbasic p-mastigophore	13·0–16·9 × 2·6	10·6–14·5 × 2·4–3·3	13·0–19·5 × 2·6–3·3
Microbasic amastigophore	16·3·20·8 × 3·3–4·6	14·5–19·9 × 3·3–4·6	16·3–21·5 × 4·0

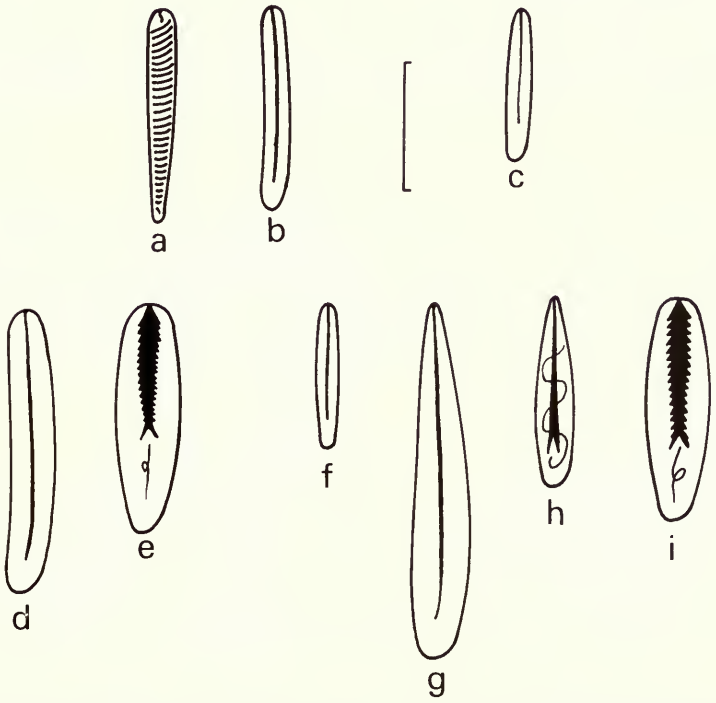

Fig. 33 *Neocondylactis singaporensis* gen. nov., sp. nov., nematocyst signature (see Table 20). *Tentacle* (a) spirocyst, (b) basitrich. *Column* (c) basitrich. *Actinopharynx* (d) basitrich, (e) microbasic amastigophore. *Filament* (f-g) basitrichs, (h) microbasic p-mastigophore, (i) microbasic amastigophore. Scale: (a-i) = 10 μm.

each side; supported by directives. Retractor muscles diffuse, strong; parietobasilar and basilar muscles present. Marginal stoma large, oral stoma small. Sphincter weak to strong, diffuse (Fig. 32b). Circular muscle folds of column low, thicker near verrucae and in sections of well extended specimens apparently forming small sphincters at bases of verrucae (Fig. 32c) which are concentrations of circular muscle round verrucal depressions. In contracted specimens verrucae appearing normal in section. *Cnidome*. See Table 20 and Figure 33. *Colour*. Column flesh colour to translucent white near base grading to greenish-white near margin. Prominent brown or green vertical lines along the mesenterial insertions. Verrucae white to off-white. Tentacles with two longitudinal brown or green lines on either side, with white or translucent spots between.

DISTRIBUTION. Recorded only from Singapore (present material).

HABITAT. Above MLTL in sand and mud, with base attached to small stones and disk lying on surface of substrate with outspread tentacles.

REMARKS. *Neocondylactis singaporensis* gen. nov., sp. nov., superficially resembles species of *Condylactis* Duchassaing & Michelotti, 1866: 125, which have elongate columns and verrucae on their upper parts. The species referred to *Condylactis*, however, have neither marginal spherules nor a sphincter, both of which are present in *N. singaporensis*. Other genera with partly similar characters are *Macrodactyla* Haddon, 1898: 431, and *Paracondylactis* Carlgren, 1934: 28; but *Macrodactyla* lacks a fosse and marginal spherules, and *Paracondylactis* has more mesenteries distally than proximally. Since no other described genus has the characters of the present species a new genus is proposed.

Genus ***TELACTINIA*** nov.

Anemonia: Haddon & Shackleton, 1893: 125 (part).
Actinia: Haddon, 1898: 416–418 (part).
Isactinia: Carlgren, 1947: 11; Carlgren, 1949: 55.
non *Isactinia* Carlgren, 1900: 53.

NOMENCLATURE. The genus name *Telactinia* is derived from the arabic 'telata' meaning three, the third variation on *Actinia*.

SCOPE. One species, *Anemonia citrina* Haddon & Shackleton, 1893.

DEFINITION. Actiniidae with pedal disk well developed. Body short. Column smooth, but sometimes an occasional verruca in upper part. At margin a ring of well developed, perforate, basitrichal spherules. Fosse shallow. Sphincter endodermal, diffuse-weak to minute. Oral disk in older specimens lobed. Tentacles short, tapering or of equal diameter throughout, numerous, their longitudinal muscles ectodermal. Siphonoglyphs one or two, pairs of directives nil to two. Many more mesenteries at margin than at base, several pairs perfect; most, including directives, fertile. Retractors diffuse. Parietobasilar muscles weak. Basilar muscles present. Cnidome: spirocysts, basitrichs and microbasic amastigophores.

TYPE SPECIES. *Anemonia citrina* Haddon & Shackleton, 1893: 125.

REMARKS. The genus *Isactinia* was introduced by Carlgren (1900: 53) to accommodate *I. badia* Carlgren, 1900: 53–55, but later (Carlgren, 1947) he referred this species to the genus *Anthostella* Carlgren, 1938: 38. *Anthostella* had the same number of mesenteries distally as proximally, and had atrichal marginal spherules between which were spherules without atrichs. Carlgren's (1900) definition of *Isactinia* mentioned that the mesenteries were numerous. He noted fifty pairs of mesenteries (i.e. 100 mesenteries) to 107 tentacles, indicating that the numbers of mesenteries at base and margin were about the same. *I. citrina* has 48 pairs of mesenteries at the base to 400 or more tentacles, indicating a difference of almost two cycles between base and margin (Carlgren, 1947). The two species differ sufficiently for it to seem appropriate now to establish a new genus to accommodate one of them.

The genus *Anthostella* now seems referable to *Isactinia* as defined in Carlgren, 1900, and *Anthostella* and *Isactinia* are probably referable to *Anthopleura* (p. 238). The species originally

included in *Isactinia* have the same number of mesenteries at margin and base, a smooth column with more or less distinct longitudinal rows of spots, and atrichal marginal spherules. As just mentioned the species which Carlgren (1947) later referred to *Isactinia*, however, have more mesenteries at margin that at base. *Isactinia* Carlgren, 1900, was defined differently and it seems consistent to propose a new genus to include some of the species referred to *Isactinia* today. The genus *Telactinia* nov. is proposed to embrace the single known species having more mesenteries distally than proximally.

Telactinia gen. nov. ***citrina*** (Haddon & Shackleton, 1893)
Figs 34–35

Anemonia citrina Haddon & Shackleton, 1893: 125; Stephenson, Stephenson & Tandy, 1931: 57.
Actinia citrina: Haddon, 1898: 416–418, pl. 22, figs 1–2, pl. 26, figs 1–5.
Isactinia ignota Carlgren, 1947: 11; Carlgren, 1950*b*: 434–436, text-figs 7–10.
Isactinia citrina: Carlgren, 1949: 55.
Isactinia lobata Carlgren, 1950*b*: 436–437, text-fig. 11.

MATERIAL EXAMINED. Singapore: Horse Shoe Reef, 1 specimen, 22 Feb 1970, BMNH 1983.11.18.24; Pulau Hantu, 3 specimens, 5 May & 17 Sep 1970, BMNH 1983.11.18.22–23, 25; Cyrene Reef, 1 specimen, 12 Oct 1969, BMNH 1983.11.18.20.

DESCRIPTION. Column mostly smooth but occasional verrucae present near margin, in one specimen a single row of verrucae. At margin a circle of large, prominent, basitrichal spherules, often irregularly arranged, on parapet. Shallow fosse present. Tentacles about 400, in several circles near outer edge of disk; short, tapered, or of equal diameter throughout, tips blunt-rounded or expanded into small spheres, but not capitate. Margin and outer part of disk often deeply folded. Centre of disk flat with small mouth. Pedal disk wider than column. *Anatomy*. Although tentacles may appear capitate, no terminal concentration of nematocysts on tentacle; nematocysts at tip same type and size range as elsewhere in tentacle. Thus tentacles desribed as not capitate, terminal expansions due to contraction or weaker mesogloea. Tentacles arranged hexamerously, in at least seven cycles, or irregularly. Mesenteries arranged hexamerously, or irregularly with more mesenteries on one side than other. One specimen with 44 pairs of mesenteries at centre of

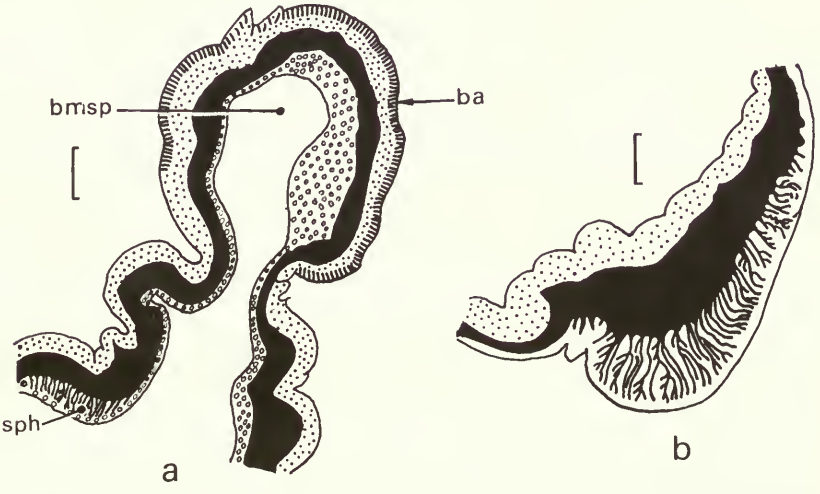

Fig. 34 *Telactinia* gen. nov. *citrina*. Vertical sections to show (a) basitrichal marginal spherule, (b) sphincter muscle, BMNH 1983.11.18.24. Scale: (a) = 150 µm, (b) = 50 µm. (ba basitrichs, bmsp endocoel of bastrichal marginal spherule, sph sphincter. Stippled, ectoderm; black, mesogloea; white, endoderm; circles, zooxanthellae in endoderm.)

column, 18 pairs on one side and 26 on the other. Two siphonoglyphs supported by directives in all specimens. At centre of column four cycles of mesenteries present, sometimes with one or two additional pairs of a 5th cycle; at margin six cycles. Most 5th cycle mesenteries extending for short vertical distance before becoming reduced to no more than a line that may reach base; 6th cycle mesenteries ceasing abruptly and little more than gussets but representing a complete cycle more at margin than at base. First four cycles fertile, including directives; up to 24 pairs perfect. Retractor muscles strong-diffuse, parietobasilar muscles weak, basilar muscles well developed. Oral and marginal stomata present. Endocoelic perforate basitrichal marginal spherules occurring over all major endocoels, with some on endocoels of younger mesenterial pairs. One specimen with 110 spherules, including 14 over 5th cycle endocoels. Basitrichs here extraordinarily numerous and densely packed, recalling arrangement of atrichs in atrichal spherules (Fig. 34a). Sphincter usually uniform between specimens, weak-diffuse (Fig. 34b). Zooxanthellae in endoderm of tentacles and disk. *Cnidome*. See Table 21 and Figure 35. *Colour*. Column off-white with some irregular green patches; marginal spherules white; disk brown to greenish-brown with white radial markings; tentacles brown with translucent white band near tip, which is often bright green.

Table 21 Size ranges of cnidae of *Telactinia* gen. nov. *citrina* (in μm).

	Localities of specimens			
Location/ Type of cnida	Cyrene reef (BMNH 1983.11.18.20)	Horseshoe reef (BMNH 1983.11.18.24)	Pulau Hantu (SW) (BMNH 1983.11.18.22)	Pulau Hantu (SW) (BMNH 1983.11.18.25)
Tentacle				
Spirocyst	13·2–26·5 × 2·0–5·3	20·0–26·5 × 3·3–4·6	13·3–26·5 × 2·6–4·6	12·0–29·8 × 2·6–5·3
Basitrich	15·2–20·0 × 2·6–3·3	15·2–18·5 × 2·6–3·3	15·2–18·5 × 2·6–3·3	8·0–24·5 × 2·6–3·3
Column				
Basitrich	20·0–23·2 × 2·6	20·5–25·8 × 2·0–2·6	18·5–23·8 × 2·6	18·5–27·8 × 2·6–3·3
Actinopharynx				
Basitrich	16·6–22·5 × 2·6–4·0	16·6–22·5 × 3·3–4·0	16·6–23·2 × 4·0	17·2–23·2 × 2·6–3·3
Microbasic amastigophore	23·2–24·5 × 4·0–6·0	20·0–23·8 × 4·0–5·3	. . .	23·8–27·8 × 4·0–4·6
Filament				
Basitrich	11·3–13·3 × 2·0	9·3–11·3 × 2·0	8·0–11·3 × 2·0	10·0–11·3 × 2·0
Basitrich	27·8–35·6 × 4·0–4·6	26·5–30·4 × 3·3–4·0	26·5–29·8 × 4·0–4·6	24·5–33·0 × 3·3–4·0
Microbasic p-mastigophore	11·3–18·5 × 2·6–3·3	13·3–16·6 × 2·6–3·3	13·3–16·6 × 3·3–4·0	12·0–19·2 × 2·6–3·3
Microbasic amastigophore	20·0–23·2 × 4·0–4·6	16·6–23·2 × 3·3–4·6	20·0–23·2 × 4·0–4·6	21·2–26·5 × 3·3–4·6

DISTRIBUTION. Reported from Torres Strait (Haddon & Shackleton, 1893, as *Anemonia citrina*), Great Barrier Reef (Carlgren, 1950*b* as *Isactinia citrina*, *I. lobata*, and *I. ignota*), and Singapore (present material).

HABITAT. Isolated specimens on coral stems.

REMARKS. From the descriptions of this species by Haddon & Shackleton (1893) and Haddon (1898) it is clear that the present material is identical with theirs. Haddon's (1898) specimens had a smooth column, many well defined marginal spherules, a folded margin in older specimens, a diffuse sphincter, and more mesenteries distally than proximally. There were 200 tentacles but 60–70 pairs of mesenteries. The number of mesenteries noted would depend on the position of the transverse sections, but a slightly larger difference might be expected. Haddon found one pair of directives but did not record the presence of siphonoglyphs. All the present specimens had two

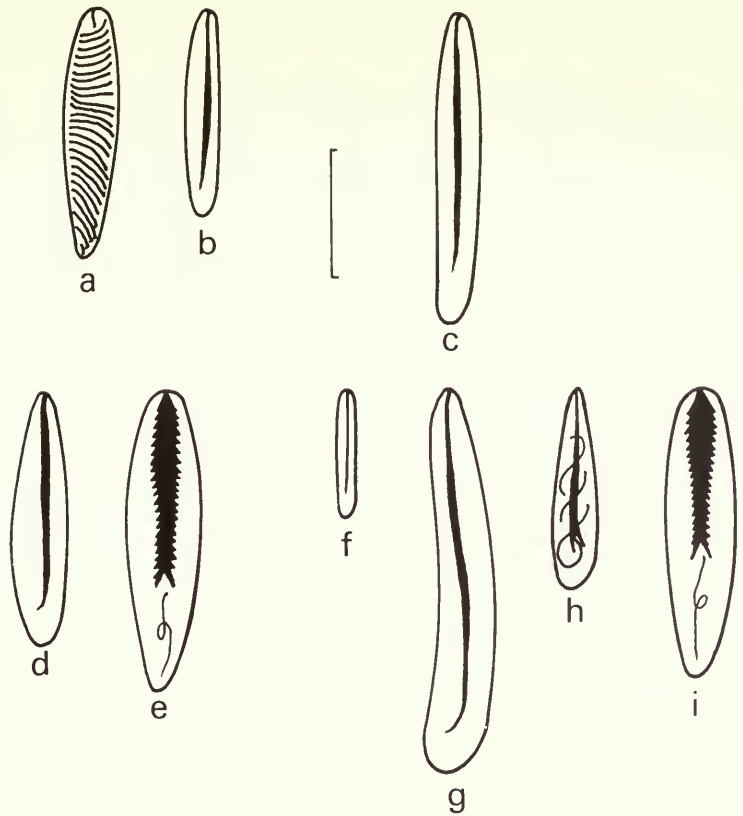

Fig. 35 *Telactinia* gen. nov. *citrina*, nematocyst signature (see Table 21). *Tentacle* (a) spirocyst, (b) basitrich. *Column* (c) basitrich. *Actinopharynx* (d) basitrich, (e) microbasic amastigophore. *Filament* (f-g) basitrichs, (h) microbasic p-amastigophore, (i) microbasic amastigophore. Scale: (a-i) = 10 μm.

Table 22 Comparison between cnida type and size in *Telactinia citrina* gen. nov. and *Isactinia* species (in μm).

Location/ Type of cnida	*Telactinia citrina* (present material)	*Isactinia ignota* (Carlgren 1950*b*)	*Isactinia lobata* (Carlgren 1950*b*)	*Isactinia olivacae* (Parry 1951)*
Tentacle				
Spirocyst	12·0–26·5 × 2·6–5·3	...	...	...
Basitrich	15·2–20·0 × 2·6–3·3	14·1–19·7 × 2·8–3·5	15·5–18·3 × 2·5–3·0	15·5–25·4 × 3·0
Column & spherule				
Basitrich	18·5–27·8 × 2·6–3·3	18·3–26·0 × 2·5–3·0	19·7–26·8 × 2·4–2·8	14·0–17·0 × 2·5
Actinopharynx				
Basitrich	16·6–23·2 × 2·6–4·0	16·8–22·6 × 2·8–3·5	18·3–22·6 × 3·0–3·5	19·7–24·0 × 3·5
Microbasic amastigophore	20·0–27·8 × 4·0–6·0	16·9–21·8 × 4·2–5·6	...	17·0 × 3·5 (1 only)
Filament				
Basitrich	8·0–13·3 × 2·0	14·0–19·0 × 2·8	10·0 × 1·5	11·3–12·7 × 4·0
Basitrich	24·5–35·6 × 3·3–4·6	27·0–32·4 × 2·5–4·2	21·0–24·0 × 2·8	19·7–22·6 × 4·5
Microbasic p-mastigophore	11·3–19·2 × 2·6–4·0	...	...	...
Microbasic amastigophore	16·6–26·5 × 3·3–4·6	14·0–22·4 × 4·2–5·6	18·3–21·1 × 4·2	17·0–22·6 × 3·5–4·5

*Carlgren's measurements from Parry's material (Carlgren, 1954: 593).

siphonoglyphs. The generic definition is here constructed to include specimens with an irregular number of directives and siphonoglyphs. Haddon & Shackleton (1893) referred the species to the genus *Anemonia*, but that is inappropriate if *Anemonia* is defined as comprising species with atrichal marginal spherules and more mesenteries proximally than distally. Since *T. citrina* has more mesenteries distally, *T. citrina* should then not be referred to *Actinia* as it was by Haddon (1898), since that genus comprises species having atrichal spherules in the fosse and the same number of mesenteries distally and proximally. The present specimens from Singapore are, therefore, referred to a new genus *Telactinia* gen. nov. (see above).

Carlgren (1950*b*) separated *Isactinia ignota* from *T. citrina* on the form of the sphincter. In Carlgren's sections the sphincter superficially differed from the structure illustrated by Haddon (1898, pl. 26, fig 2), but in detail it was similar.

The different sphincters of four specimens differing in size are shown in Carlgren's text-figures 7–10. Each illustration nevertheless depicts the same type: the example in text-figure 7 is least developed and the one in text-figure 8 the most developed and similar to a well developed sphincter of *T. citrina*. Carlgren (in Stephenson, *et al.*, 1931: 57) initially suggested that *I. ignota* was conspecific with *T. citrina* but when describing it (Carlgren, 1947) he proposed a separate species. It is considered here to be conspecific with *T. citrina*.

Isactinia lobata Carlgren, 1950*b*: 436–437, was proposed on the grounds that Stephenson had informed Carlgren that the tentacles tended to be capitate compared with filiform in *I. citrina* and *I. ignota*. The sphincter was weak. He gave details of the nematocyst types and size ranges which are similar to those of *T. citrina* (see Table 22). In view of these similarities *I. lobata* is here referred to *T. citrina*.

Material of *Isactinia olivacea* Parry, 1951: 108, was examined by Carlgren (1954: 593–594) who found that while one specimen could be referred to *Isactinia* the other was *Cnidopus verater* (Drayton, 1846). He listed the types and size ranges of the nematocysts (Table 22). The basitrichs in the filaments were smaller in size than those of *I. citrina*. *I. olivacea* should perhaps be referred to *Telactinia*, possibly as a second species, but further examination is first required to confirm the ratio of the number of tentacles to the number of mesenteries at the base.

Carlgren (1945: 10) described the nematocysts of *I. mesembryanthemum* (Ehrenberg, 1834: 36) and it appears that it should not be referred to *Isactinia* since it had atrichs in the spherules. All other species at one time referred to *Isactinia* have subsequently been shown to be referrable to different genera.

Family **STICHODACTYLIDAE** Andres, 1883

Definition. Endomyaria with well developed pedal disk. Column smooth or with suckers or verrucae. *Ectoderm of column always containing microbasic amastigophores (p-mastigophores).* Tentacles long or reduced, wart-shaped, or short, one per exocoel, located marginally; some older endocoels having one tentacle or a number of tentacles arranged in radial rows. Sphincter endodermal, diffuse to circumscribed, weak to absent. Longitudinal muscles of tentacles and radial muscles of oral disk ectodermal. Pairs of perfect mesenteries numerous, stronger ones with or without directives, fertile. Retractor muscles diffuse, weak to strong. Cnidome: spirocysts, atrichs, basitrichs, microbasic amastigophores and microbasic p-mastigophores.

Remarks. Dunn (1981: 37) re-employed the name Stichodactylidae Andres, 1883, in place of Stoichactiidae Carlgren, 1900: 72, on the grounds of priority. She included the genera *Heteractis* Milne Edwards & Haime, 1851 (including the congeneric *Radianthus* Kwietniewski, 1896) and *Stichodactyla* Brandt, 1835 (including the congeneric *Stoichactis* Haddon, 1898) within its scope.

However, *Heteractis aurora* Quoy & Gaimard, 1833: 141, the type species of the genus *Heteractis* Milne Edwards, 1857: 10, differs from other species referred to the genus *Radianthus* Kwietniewski, 1896: 389, in having macrobasic amastigophores in the ectoderm of the tentacles and column, and in the actinopharynx and filaments (England, in press). *Radianthus* is, therefore, considered a valid genus with *Radianthus kukenthali* Kwietniewski, 1896: 389, the type species.

The Stichodactylidae is separated from the Actiniidae mainly on the presence of more than one tentacle communicating with some or all of the older endocoels in the former compared with the

latter, in which there is only one tentacle in each endocoel. Stephenson (1922: 298) included the genus *Antheopsis* (Simon, 1892) Carlgren, 1900, in the Stoichactiidae, so as to include species that had one or only a few tentacles communicating with the older endocoels as opposed to those having them in definite radial rows. My efforts to trace the Simon, 1892, work have been unsuccessful. It was cited by Carlgren, 1900, as an Inaugural Dissertation from the University of Munich. The work was printed, but is not listed in the British Museum Catalogue of Printed Books and seems to have remained unpublished. Hence the genus *Antheopsis* is taken to date from Carlgren, 1900, which included a definition, pending clarification of the availability of the name as employed by Simon. *Proof note: A photocopy of Simon's work has now been obtained by the British Museum (Natural History).*

Carlgren (1949: 73) did not support this view and referred *Antheopsis* Simon, 1892, to the genus *Radianthus* Kwietniewski, 1896. However, elsewhere Carlgren (1950*a*: 139) recognized the genus *Antheopsis* in order to accommodate a then newly described species, *A. australiensis* Carlgren, 1950*a*. Examination of specimens referred by Carlgren to *A. australiensis* failed to find microbasic amastigophores in the column or tentacle ectoderm. The species is probably referrable to *Aulactinia*. Carlgren, (1900: 104) repeated his earlier comments about *A. koseirensis* (Klunzinger, 1877) that only one tentacle communicates with even the strongest endocoels. It is possible that more than one tentacle occurs occasionally on the older endocoels in *A. koseirensis* but specimens from Egypt and Aden examined during the present work did not have secondary tentacles (unpublished data). Carlgren (1900: 104; 1950*a*: 141) stated that he considered *Antheopsis* to be a stichodactylid genus differing from actiniids in having numerous bifid tentacles.

A previously unrecognized character may be used to distinguish the Stichodactylidae from the Actiniidae. In the Stichodactylidae, ectodermal microbasic amastigophores are present in either the column or the tentacles or in both. The definition of the Stichodactylidae is modified to include this character. Species in which they are absent from these regions are referred to the Actiniidae.

This type of nematocyst is known to occur in only one genus in the Actiniidae, *Entacmaea* Ehrenberg, 1834. The presence of microbasic amastigophores in the Stichodactylidae may have been overlooked because they are often scarce. However, they are usually larger than those in the actinopharynx or filaments and so are conspicuous in squashes and in sections. Although they usually occur in the ectoderm of both tentacles and column there are at least two species which lack them in the tentacles. *Antheopsis concinnata* Lager, 1911, and *Stichodactyla helianthus* (Ellis, 1768) (unpublished observations).

Although Dunn (1981: 80) did not report microbasic amastigophores or p-mastigophores from the column of *Stichodactyla helianthus*, I have found them in a specimen from Andros in

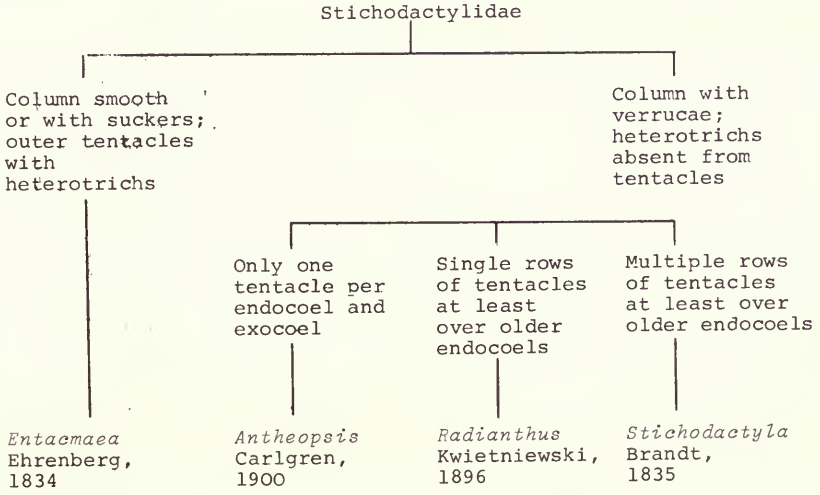

Fig. 36 Key to the genera of the Stichodactylidae.

the Caribbean provided by Dr G. F. Warner, University of Reading. The size range was 27·6.–34·8 × 5·3–6·0 μm.

Dunn (1981: 21) recorded the presence of microbasic amastigophores on the column of *Entacmaea quadricolor* (Rueppell & Leuckart, 1828). I have found them in the tentacles as well and also observed heterotrichs in the outer tentacles (see below). Dunn discovered small secondary tentacles occurring occasionally over some of the older endocoels. These were found also on a specimen from Singapore (BMNH 1984.2.15.1, see below). Assessment of these characters suggests that *Entacmaea* has more affinity with the Stichodactylidae than with the Actiniidae and it is here transferred to the Stichodactylidae.

Since Carlgren (1950*a*: 141) reinstated the genus *Antheopsis* a second species has been reported that is referred to that genus, and it is redefined here.

A key to the genera of the Stichodactylidae is given in Figure 36.

Genus *ANTHEOPSIS* Carlgren, 1900

Antheopsis (Simon, 1892: 30); Carlgren, 1900: 104; Carlgren, 1950*a*: 140; Stephenson, 1911: 300.
Bunodes: Klunzinger, 1877: 77; Andres, 1883: 451.
Radianthus: Carlgren, 1949: 73 (part).
Heteractis: Dunn, 1981: 38 (part).

Nomenclature. Availability of this genus is discussed on page 273.

Definition. Stichodactylidae with wide pedal disk. Oral disk sometimes lobed. Column with verrucae in upper parts and sometimes suckers below, extending to limbus. Only one tentacle communicating with older endocoels: occasionally one or two secondary tentacles, but never forming radial rows. Sphincter circumscribed through diffuse to absent. Mesenteries hexamerously or irregularly arranged; same number proximally and distally; all stronger ones fertile. Siphonoglyphs varied in number, with or without supporting directives. Retractor muscles diffuse, parietobasilar and basilar muscles present. Cnidome: spirocysts, basitrichs, microbasic amastigophores and p-mastigophores.

Type Species. *Bunodes koseirensis* Klunzinger, 1877, by original designation.

Antheopsis malayensis sp. nov.
Figs 37–38

Material Examined. Holotype: Malaysia, Pulau Tioman, BMNH 1984.2.9.1. Paratypes: 7 specimens, same locality, 27 March 1970, BMNH 1984.2.9.2–8.

Description. Column cylindrical to trumpet shaped, disk wider than centre of column (Fig. 37a). Margin crenulate, no true spherules. Verrucae present on margin and upper column in vertical rows of about 10, over both endo- and exocoels; lower down column reduced to suckers, recalling *Sagartia*. Near limbus suckers scattered over column. Fosse shallow. Tentacles mostly tapered, with blunt tips, sometimes inflated subdistally giving capitate appearance. Up to 65 tentacles, one communicating with each endo- and exocoel. Base narrower than disk. Column short. Average extended height 15–25 mm, disk diameter 25 mm. *Anatomy*. Siphonoglyphs 2–10, not supported by directives. Mesenteries irregularly arranged with about twelve pairs perfect; all youngest fertile, most bearing filaments with ciliated tracts; same number distally and proximally, but in centre of column youngest cycles small. No directives. Large oral and small marginal stomata present. Retractor muscles diffuse-weak, parietobasilar and basilar weak. No sphincter (Fig. 37b). Zooxanthellae present in endoderm of tentacles, disk and column. *Cnidome*. See Table 23 and Figure 38. *Colour*. Light green throughout.

Distribution. Known from type locality only.

Habitat. Densely packed on stems of dead stags-horn coral (*Acropora* sp.) 1 m below MLTL. Also associated with *Mesactinia ganensis* gen. nov., sp. nov. (p. 263) on same coral. Whether the two

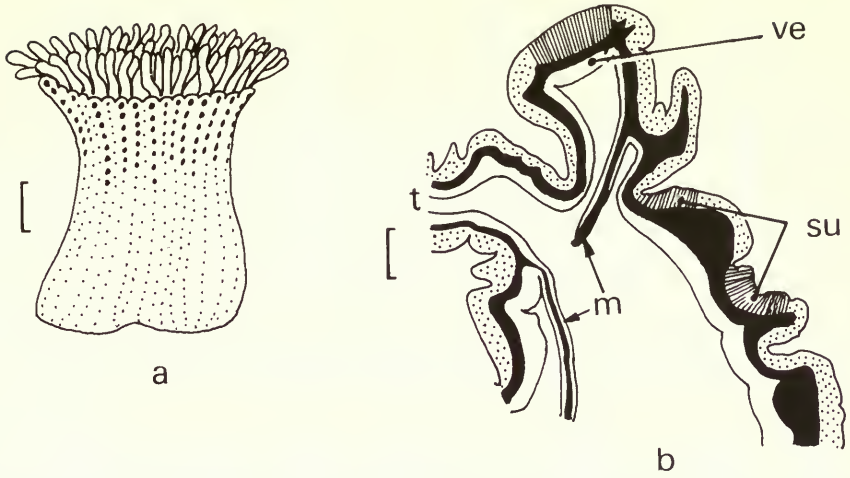

Fig. 37 *Antheopsis malayensis* sp. nov. BMNH 1984.2.9.1–8. (a) General appearance, side view. (b) Vertical section through margin showing verrucae and suckers; note absence of sphincter muscle. Scale: (a) = 4 mm, (b) = 100 μm. (m mesentery, su suckers, t tentacle, ve verruca. Stippled, ectoderm; black, mesogloea; white, endoderm; hatched, adhesive areas.)

Table 23 Size ranges of cnidae of *Antheopsis malayensis* sp.nov. (in μm).

	Locality of specimens		
Location/ Type of cnida	Pulau Tioman 'Holotype'	Pulau Tioman (BMNH 1984.2.9.2)	Pulau Tioman (BMNH 1984.2.9.3)
Tentacle			
Spirocyst	12·0–24·0 × 2·4–3·6	14·6–26·5 × 2·0–2·6	14·6–29·8 × 2·0–4·0
Basitrich	15·6–28·8 × 2·4–3·0	16·6–17·1 × 2·0–2·6	20·0–26·5 × 2·6–3·3
Microbasic amastigophore	24·0–30·0 × 4·0–6·0	21·2–25·2 × 4·6–5·3	21·2–28·5 × 4·6–5·3
Column			
Spirocyst	24·0–25·2 × 3·0	23·2–28·5 × 2·6	21·8–27·8 × 3·3
Basitrich	18·0–22·8 × 2·4	16·6–23·2 × 2·0–2·6	21·2–25·2 × 2·6
Microbasic amastigophore	24·0–26·4 × 4·8–6·0	...	22·8–28·5 × 4·6–5·3
Actinopharynx			
Basitrich	9·6–16·8 × 2·0	...	15·2–16·6 × 2·0
Basitrich	20·4–28·8 × 3·0	23·8–29·8 × 2·6	26·5–29·8 × 3·3
Microbasic amastigophore	19·2–24·0 × 4·2	23·2–25·2 × 4·6	22·5–27·6 × 4·6–5·3
Filament			
Basitrich	14·6–17·2 × 2·0	13·3–18·5 × 2·0	14·6–16·6 × 2·0
Basitrich	15·2–23·2 × 3·3	17·9–20·0 × 2·6–3·3	13·3–20·0 × 3·3–4·0
Basitrich	25·8–32·3 × 5·3–6·6	23·2–33·0 × 4·0–5·3	29·8–36·3 × 4·6–6·0
Microbasic amastigophore	21·8–27·1 × 4·6–5·3	21·2–26·5 × 4·0–4·6	21·2–26·5 × 4·0–4·6

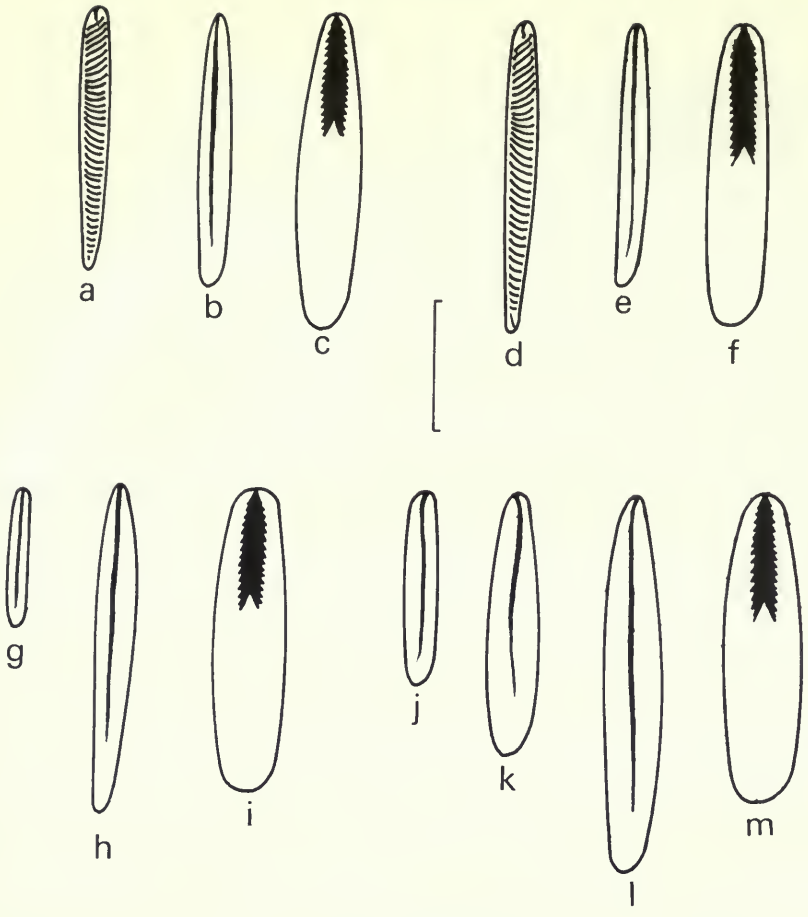

Fig. 38 *Antheopsis malayensis* sp. nov., nematocyst signature (see Table 23). *Tentacle* (a) spirocyst, (b) basitrich, (c) microbasic amastigophore. *Column* (d) spirocyst, (e) basitrich, (f) microbasic amastigophore. *Actinopharynx* (g-h) basitrichs, (i) microbasic amastigophore. *Filament* (j-l) basitrichs, (m) microbasic amastigophore. Scale: (a-m) = 10 μm.

species keep in separate groups or are mingled is not known. The species was not discovered until noticed among preserved specimens of *M. ganensis*.

Remarks. The presence of microbasic amastigophores in the tentacles and on the column indicates affinity with species of Stichodactylidae. The single tentacle per endo- and exocoel and the verrucated column suggest that the present material should be referred to the genus *Antheopsis*. Stephenson (1922: 300) listed 10 species of *Antheopsis* but several have the tentacles in radial rows and are referred to *Radianthus*, and another, *A. carlgreni* Lager, 1911, is referred to *Entacmaea*. The three species *A. koseirensis* (Klunzinger, 1877), *A. glandulosa* Lager, 1911, and *A. kwietniewski* Lager, 1911, differ from the present material in having regularly arranged mesenteries and a sphincter. It is, therefore, proposed to refer the present material to a new species, *Antheopsis malayensis* sp. nov.

Genus *ENTACMAEA* Ehrenberg, 1834

For synonymy see Dunn, 1981: 13–14.

Definition. Stichodactylidae with well developed pedal disk. Column smooth or with small

suckers in upper part. Margin distinct, without spherules; fosse deep. One tentacle per endocoel and per exocoel, but in large specimens a small subsidiary tentacle may occasionally be found close to or on the tentacles of older cycles. Subsidiary tentacles never forming radial rows. Ectoderm of outer tentacles with heterotrichs. Longitudinal muscles of tentacles and radial muscles of oral disk ectodermal. Siphonoglyphs varied in number, normally supported by directives. Perfect mesenteries numerous; all stronger ones, including directives, fertile. More mesenteries at margin than at base. Sphincter weak to strong, diffuse; rarely absent. Cnidome: spirocysts, heterotrichs, basitrichs, microbasic amastigophores and p-mastigophores.

TYPE SPECIES. *E. quadricolor* Ehrenberg, 1834, by monotypy.

Entacmaea quadricolor Ehrenberg, 1834

For synonyms see Dunn, 1981: Fig. 39.

MATERIAL EXAMINED. Red Sea: Egypt, 2 specimens, coll. Dr F. A. Shoukr. Singapore: Pulau Hantu, 1 specimen, 18 Jan 1970, BMNH 1984.2.15.1; Pulau Biola, 1 specimen, 13 Sep 1970, BMNH 1985.2.13.7.

REMARKS. There is little to add to the comprehensive description given by Dunn (1981: 15–28, figs 5–10). In the present material there are small suckers scattered over the upper part of the column, and additional types of nematocysts in certain areas. The suckers are not visible in whole preserved specimens but are easily seen in histological sections and resemble those depicted by Stephenson (1928: 13–14, fig. 8c) in *Sagartia elegans* Dalyell, 1848.

There is a dense concentration of nematocysts inside the fosse and over the margin. Most are basitrichs, a few are microbasic amastigophores, and spirocysts are absent. The nematocysts are

Table 24 Size ranges of cnidae of *Entacmaea quadricolor* (in μm).

	Locality of specimens			
Location/ Type of cnida	Egypt (Red Sea) Coll. F. A. M. Shoukr	Egypt (Red Sea) Coll. F. A. M. Shoukr	Pulau Hantu (BMNH 1984.2.15.1)	Pulau Biola (BMNH 1985.2.13.7)
Tentacles				
Spirocyst	18·5–39·6 × 2·6–5·3	18·5–35·0 × 2·0–6·0	16·6–33·7 × 2·0–4·6	18·0–35·0 × 2·6–4·0
Basitrich	10·6–12·6 × 2·6–3·0	11·3–14·6 × 3·3	8·6–10·0 × 2·0	...
Basitrich	18·5–26·5 × 3·3–6·0	18·5–25·8 × 3·3–5·3	16·6–25·2 × 4·6–5·3	17·2–27·8 × 4·0–5·3
Heterotrich	24·5–30·4 × 4·0–4·6	25·2 × 4·6 (1 only)	23·8–27·8 × 4·0–4·6	20·5–29·8 × 3·3
Microbasic amastigophore	28·5–37·6 × 5·3–6·6	29·1–36·3 × 5·3–6·6	33·0–44·9 × 6·0–6·6	28·5–35·0 × 5·3–6·0
Column				
Basitrich	11·3–12·0 × 2·0–2·6	10·6–13·3 × 2·0–2·6	10·0–11·3 × 2·0	9·3–12·0 × 2·0
Basitrich	21·8–26·5 × 2·6–3·3	17·9–26·5 × 2·6–4·0	17·9–27·7 × 3·3	18·5–24·5 × 2·6–3·3
Microbasic amastigophore	33·0–41·6 × 5·3–6·6	31·7–41·0 × 6·6–7·2	39·6–50·2 × 6·0–7·2	30·1–42·9 × 5·3–6·6
Actinopharynx				
Basitrich	18·5–26·5 × 4·0–4·6	18·5–25·8 × 4·0–4·6	18·5–26·5 × 3·3–4·0	20·0–25·2 × 3·3–4·0
Microbasic amastigophore	26·5–29·8 × 5·3–6·0	22·5–29·8 × 6·0–6·6	30·1–38·3 × 4·6–6·6	24·5–31·1 × 4·6–5·3
Filament				
Basitrich	13·3–15·2 × 3·3–4·0	12·0–14·0 × 2·6–3·3	11·3–13·3 × 2·6	12·0–13·3 × 2·0
Basitrich	21·2–25·8 × 4·0–5·3	20·0–24·5 × 3·3	16·6–26·5 × 3·3	17·9–20·0 × 3·3
Microbasic p-mastigophore	19·2–21·8 × 5·3–6·0	20·0–22·5 × 4·6–6·0	23·2–26·5 × 4·0	20·0–23·2 × 4·0–4·6
Microbasic amastigophore	24·5–29·8 × 6·0–6·6	21·2–29·8 × 5·3–6·6	31·7–36·3 × 5·3–6·0	28·5–33·0 × 4·6–5·3

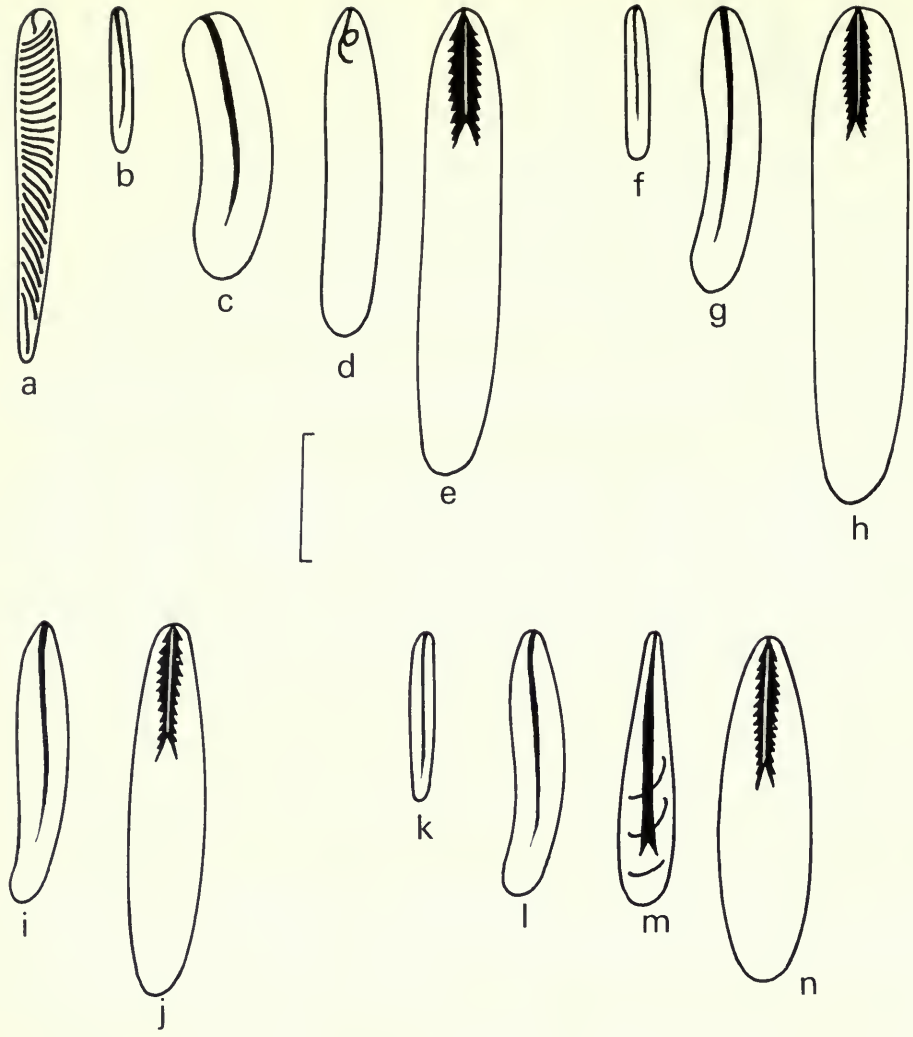

Fig. 39 *Entacmaea quadricolor*, nematocyst signature (see Table 24). *Tentacle* (a) spirocyst, (b-c) basitrichs, (d) heterotrich, (e) microbasic amastigophore. *Column* (f-g) basitrichs, (h) microbasic amastigophore. *Actinopharynx* (i) basitrich, (j) microbasic amastigophore. *Filament* (k-l) basitrichs, (m) microbasic p-mastigophore, (n) microbasic amastigophore. Scale: (a-n) = 10 μm.

closely packed as in a spherule and this feature continues around the margin. Microbasic amastigophores have been found in the ectoderm of the tentacles and the column by examination of squash preparations and serial sections. Heterotrichs have been found on some tentacles, confined mostly to the outer cycles.

Dunn (1981: 24) considered that specimens with regularly arranged mesenteries belong to the same species as those with irregularly arranged mesenteries, but it is customary to use this character to differentiate species. All specimens discussed here have a regularly arranged internal anatomy.

Cnidome. See Table 24 and Figure 39. The basitrichs of the tentacles and of the column ectoderm differ in shape from those found in the Actiniidae and Stichodactylidae. They are much broader and have a thread that is easily seen under the light microscope.

Sub-tribe **ACONTIARIA** Carlgren, in Stephenson, 1935
Family **HORMATHIIDAE** Carlgren, 1932

NOMENCLATURE. Carlgren (1949: 91) gave the authority for the Hormathiidae as Carlgren, 1925*c*, but did not indicate the publication. None of the three references given by Carlgren dated 1925 mentioned Hormathiidae. His earliest suggestion that certain genera should be separated from the Sagartiidae was Carlgren, 1928, when he placed the name Hormathiiden in brackets after Sagartiidae in the generic definitions of *Paracalliactis* Carlgren, 1928, *Calliactis* Verrill, 1869*b*, *Phelliactis* Simon, 1982, and *Chondrophellia* Carlgren, 1928. It was not until 1932 that he gave his reason. Carlgren (1932: 262) then stated that the family Chondractiniidae Stephenson, 1920: 478, which was based on the sub-family Chondractiniinae Haddon, 1889: 305, must be referred to the Hormathiidae since the genus *Chondractinia* Lutken, 1860: 190, was congeneric with *Hormathia* Gosse, 1859: 47. In fact *Chondractinia* is a *nomen nudum* since, according to Haddon, no definition was given. The correct authority for the family Hormathiidae is, therefore, Carlgren, 1932.

Genus ***Calliactis*** Verrill, 1869*b*

Priapus Forsskål, 1775: 102.
Actinia: de Blainville, 1830: 293 (part); Dana, 1846: 139 (part).
Cribrina Ehrenberg, 1834: 40.
Cribrina (Tristemma) Brandt, 1835: 293.
Calliactis Verrill, 1869*b*: 481.
Adamsia: Haddon & Shackleton, 1893: 130.

DEFINITION. Hormathiidae with well developed pedal disk. Column smooth, slightly differentiated into scapus (which has a weak cuticle) and scapulus, or undifferentiated, often thick; sometimes with numerous ectodermal invaginations which do not pierce the wall. Cinclides always present in lower part of column. Sphincter strong, mesogloeal. Tentacles rather short, tapered, more numerous than mesenteries at base, their longitudinal muscles ectodermal. Radial muscles or oral disk more or less embedded in mesogloea. Siphonoglyphs two, broad. Six pairs of perfect, sterile mesenteries. Retractor muscles diffuse, weak, parietobasilar muscles weak or well developed. Often commensal with hermit crabs. Cnidome: spirocysts, basitrichs, microbasic amastigophores.

TYPE SPECIES. *Priapus polypus* Forsskål, 1775, by present designation (p. 280).

Calliactis polypus (Forsskål, 1775)

Priapus polypus Forsskål, 1775: 102.
Actinia polypus: de Blainville, 1830: 292; de Blainville, 1834: 327.
Cribrina polypus: Ehrenberg, 1834: 40.
Actinia decorata Dana, 1846: 139; Dana, 1849, pl. 3 fig. 24; Dana, 1859: 8.
Adamsia decorata: Milne Edwards, 1857: 281.
Calliactis polypus Klunzinger, 1877: 76, pl. 5, fig. 1; Hertwig, 1882: 74–76; Carlgren, 1900: 75, pl. 1, figs 3–4; Carlgren, 1938: 76–77; Carlgren, 1949: 97; England, 1971: 23–29, pl. 1, figs A-C, pl. 2, fig. 1.
Adamsia miriam Haddon & Shackleton, 1893: 130.
Calliactis miriam Haddon, 1898: 457, pl. 23, fig 25; Stephenson *et al.*, 1931: 72; Carlgren, 1950*a*: 141–142; Carlgren, 1950*b*: 444 (part).
Calliactis armillatus Verrill, 1928: 20 (part).

MATERIAL EXAMINED. The Maldives: Gan Island, Addu Atoll, 6 specimens on 2 gastropods, 8 Mar 1970, BNMH 1985.2.13.2–6; associated with 2 specimens of *Verrillactis paguri* (Verrill, 1869*a*), BMNH 1985.2.13.1.

DESCRIPTION. For detailed description see England (1971: 23–29). The specimens from Gan were smaller than those described in that paper and had only 48 pairs of mesenteries at the centre of the column, but the main characters of the species were present.

REMARKS. A nominal species additional to those listed earlier (England, 1971) can be referred to *C. polypus*: *Actinia decorata* Dana, 1849 (= *Adamsia decorata* Milne Edwards, 1857), originally

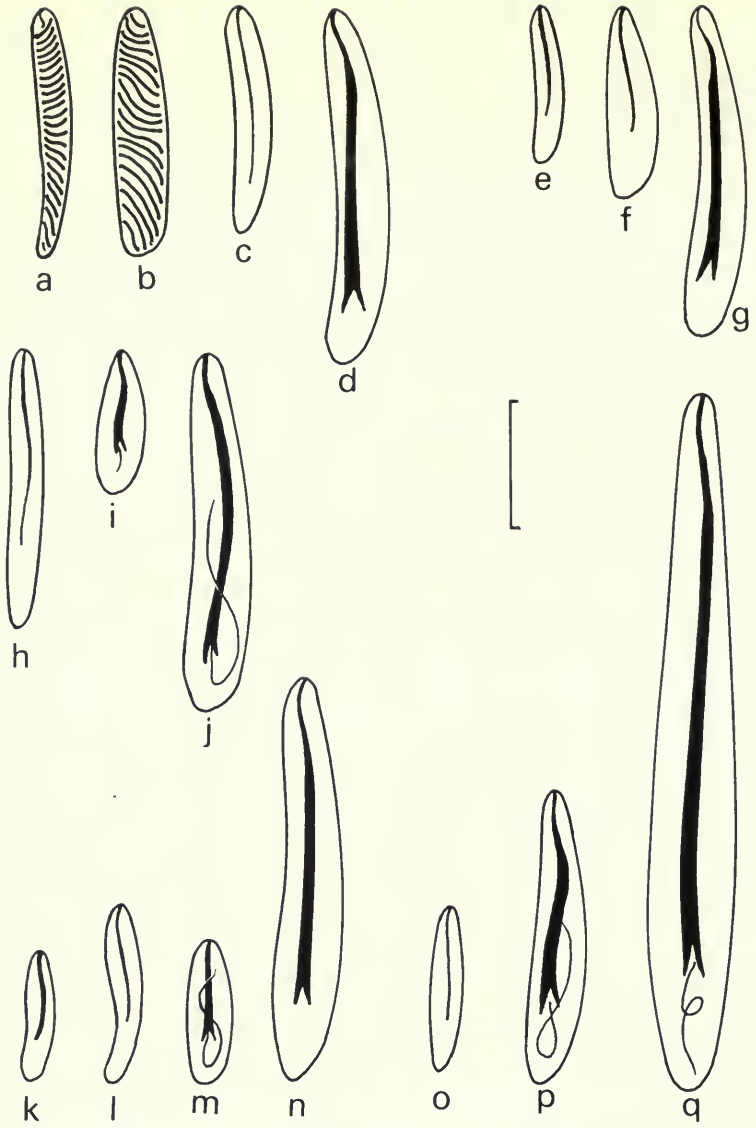

Fig. 40 *Carcinactis ichikawai*, nematocyst signature (after Uchida, 1960). *Tentacle* (a-b) spirocysts, (c) basitrich, (d) microbasic amastigophore. *Column* (e-f) basitrichs, (g) microbasic amastigophore. *Actinopharynx* (h) basitrich, (i-j) microbasic amastigophores. *Filament* (k-l) basitrichs, (m-n) microbasic amastigophores. *Acontia* (o) basitrich, (p-q) microbasic amastigophores. Scale: (a-q) = 10 μm.

found at 'Honden Island'. This species was not considered in the earlier paper because it was not then possible to determine the whereabouts of Honden Island. With the assistance of the Department of the Hydrographer of the Royal Navy, Honden Island was found to be that better known as Puka Puka in the Tuamoto group. Among the material previously examined some was collected from the same area as Dana's material and it seems more probable than before that *Actinia decorata* is conspecific with *C. polypus*. *Priapus polypus* Forsskål, 1775, is, therefore, designated type species of the genus *Calliactis* Verrill, 1869*b*.

DISTRIBUTION. Red Sea (Klunzinger, 1877), Aden (England, 1971), Mombassa (A. K. Totton coll., BMNH 1955.6.9.96–97), Chagos Archipelago (J. S. Gardiner coll., BMNH 1939.7.3.45–46), Maldives (J. S. Gardiner coll., BMNH 1939.7.3.35–38); K. W. England coll., present material, BMNH 1985.2.13.2–6), Malay Straits (Challenger coll., BMNH 1889.11.25.67), Christmas Island (BMNH 1935.3.5.1), Hawaii (Verrill, 1928), Great Barrier Reef: Low Isles (Carlgren, 1950*a*, 1950*b*), Tuamoto Archipelago (Dana, 1948, as *Actinia decorata*, and England, 1971).

Family **SAGARTIIDAE** Gosse, 1858, s.str.
Genus ***VERRILLACTIS*** England, 1971

Calliactis Verrill, 1928: 20 (part).
Verrillactis England 1971: 29.

DEFINITION. Sagartiidae with broad pedal disk. Column smooth or with ectodermal invaginations that do not pierce the column wall, divisible into scapus and scapulus. Mesenteries arranged hexamerously or irregularly, with number at base about twice that at margin; 6–12 pairs, perfect and sterile. 1–2 siphonoglyphs which may not be supported by directives. Sphincter mesogloeal,

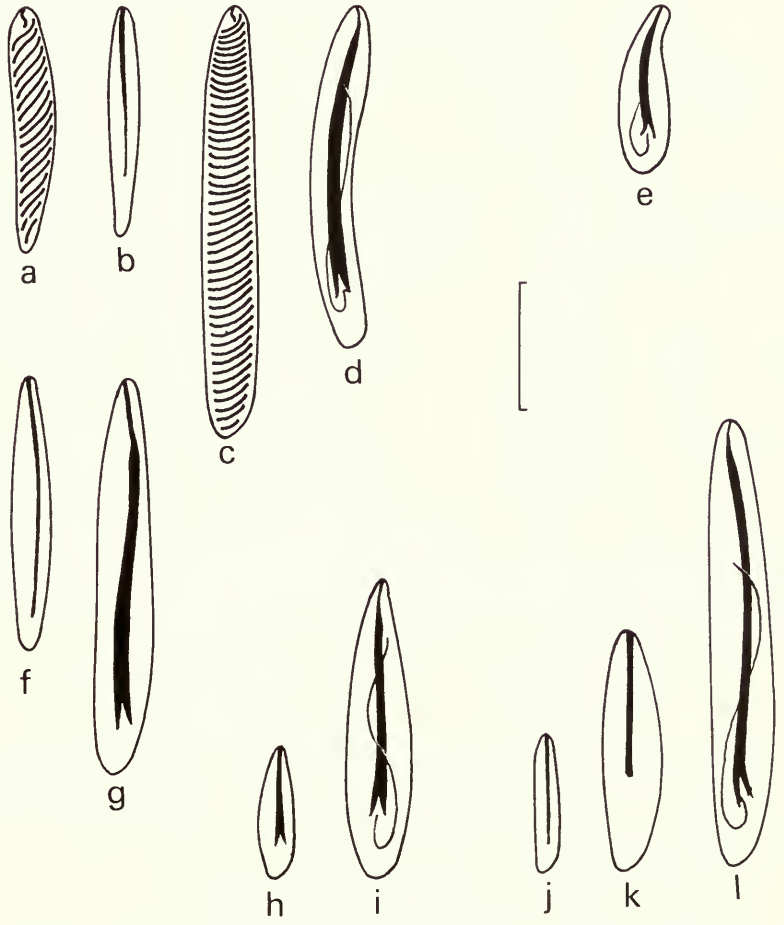

Fig. 41 *Verrillactis paguri*, nematocyst signature (after England, 1971). *Tentacle* (a) spirocyst, (b) basitrich, (c) atrich, (d) microbasic amastigophore. *Column* (e) microbasic amastigophore. *Actinopharynx* (f) bastrich, (g) microbasic amastigophore. *Filament* (h-i) microbasic amastigophores. *Acontia* (j-k) basitrichs, (l) microbasic amastigophore. Scale: (a-l) = 10 μm.

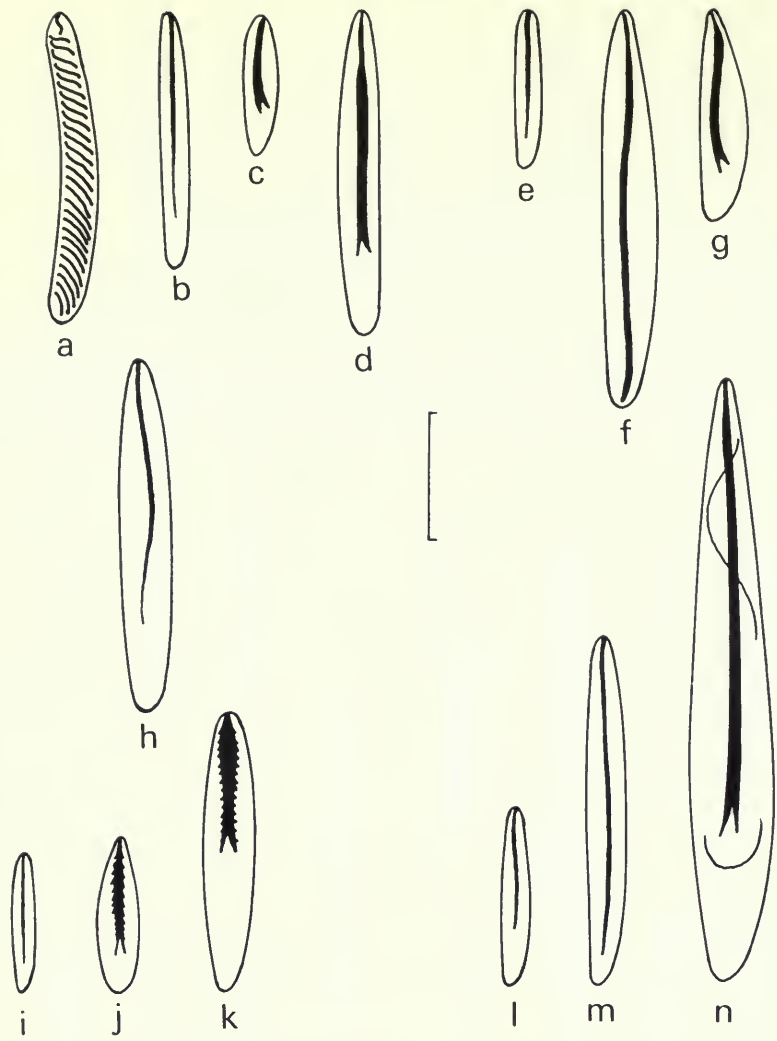

Fig. 42 *Carcinactis dolosa*, nematocyst signature (after Riemann-Zürneck, 1975). *Tentacle* (a) spirocyst, (b) basitrich, (c-d) microbasic amastigophores. *Column* (e-f) basitrichs, (g) microbasic amastigophore. *Actinopharynx* (h) basitrich. *Filament* (i) basitrich, (j-k) microbasic amastigophores. *Acontia* (l-m) basitrichs, (n) microbasic amastigophore. Scale: (a-n) = 10 μm.

strong. Cinclides absent. Tentacles: inner longer than outer, some forming catch tentacles bearing large atrichs. Acontia with three distinct types of nematocyst; *two types of basitrichs and one type of microbasic amastigophore*. Commensal with hermit crabs, often with *Calliactis polypus*. (p. 279).

Type Species. *Sagartia paguri* Verrill, 1869*a*, by monotypy.

Verrillactis paguri (Verrill, 1869*a*)

Description. For detailed description and synonyms see England (1971).

Material Examined. 2 specimens, Maldives, Gan Island, Addu Atoll, 8 Mar 1970, BMNH 1985.2.13.1.

REMARKS. At the time of the original description the presence of cinclides was in doubt. On examination of the material from Gan the absence of cinclides was confirmed.

England (1971: 33) suggested that *V. paguri* Verrill, 1869*a*, was a new combination for *Sagartia paguri* Verrill, 1869*a*. (A difficulty is that Verrill's descriptions are brief, so that they cannot easily be compared.) However, Ross and Wada (1975: 1738) found an anemone on a left chela of *Diogenes edwardsi* (Dehaan) which lacked acontia and which was probably *S. paguri* Verrill. Since Verrill (1869*a*) stated that *S. paguri* occurred on this crab it seems likely that *Verrillactis paguri* is distinct. Examinations of specimens from the crab *D. edwardsi* is desirable before a decision is made.

Riemann-Zürneck (1975: 85) suggested that the nominal genus *Verrillactis* England, 1971, should be referred to *Carcinactis* Uchida, 1960: 595. The latter stated that species referred to *Carcinactis* have the mesenteries divided into macrocnemes and microcnemes. If so, the genus would be better referred to the Isophelliidae than to Sagartiidae. Uchida's figures 4–5 indicate a clear demarcation between cycles 1–3 and 4, giving 24 pairs of macrocnemes and 24 pairs of

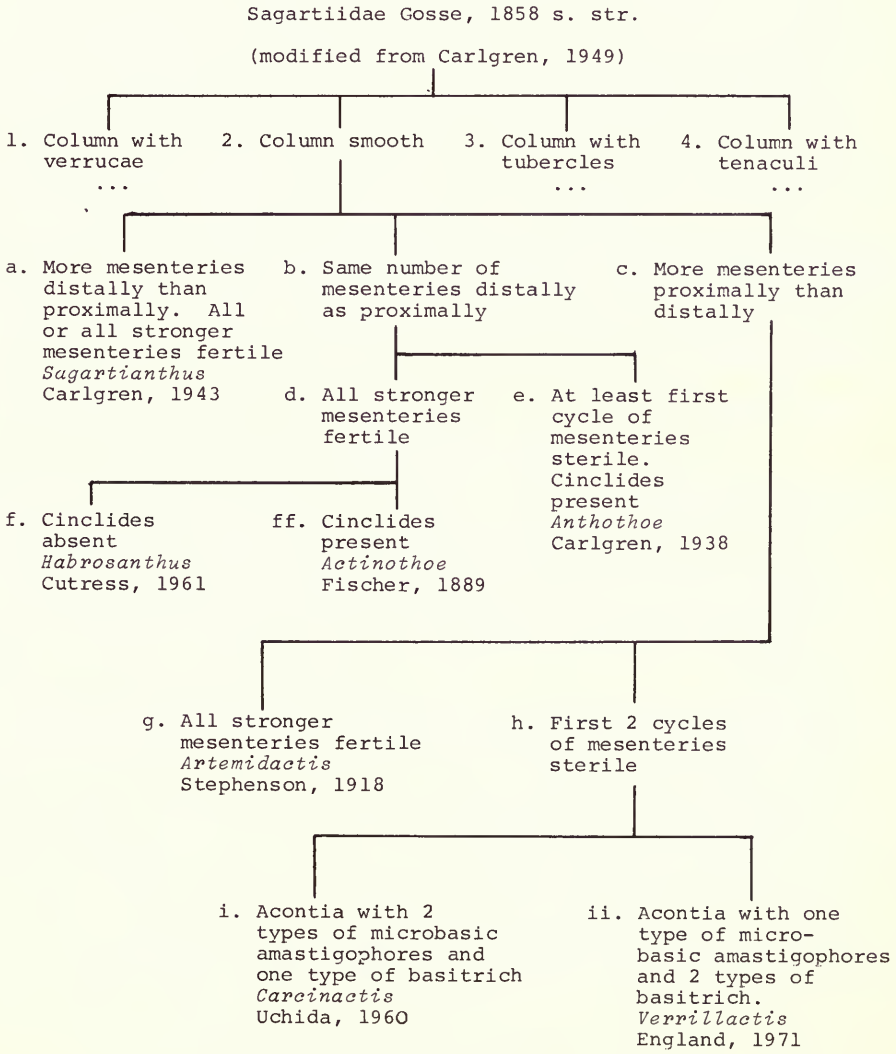

Fig. 43 Key to certain genera of the Sagartiidae.

microcnemes near the margin. These figures also illustrate a pair of directives not connected with a siphonoglyph; although Uchida specified 'siphonoglyphs two, associated with directive mesenteries'. His figure 6 did depict a siphonoglyph supported by directives, and his figure 7 showed that the 3rd, 4th and 5th cycles were successively smaller in size. Possibly the sections shown in Uchida's figures 4 & 5 had been cut through the column up into the disk, but outside the mouth, so that they would have omitted the actinopharynx and siphonoglyphs. Although the mesenteries decreased regularly in size from 1st to last cycle, this also led to their having the appearance of macrocnemes and microcnemes. *Carcinactis* is thus better referred to the Sagartiidae, as defined by Uchida, and reference to macrocnemes and microcnemes perhaps deleted from the definition.

The nematocysts of the acontia of *Carcinactis ichikawai* were illustrated by Uchida (1960: 598; fig. 1) as one type of basitrich and two types of microbasic amastigophores, suggesting that the two genera should be held distinct.

Carcinactis dolosa Riemann-Zürneck, 1975, also has two types of basitrich and one type of microbasic amastigophore in the acontia, but the larger type of basitrich differs from that in the species referred to *Verrillactis*. There is also difference in the types that occur in other parts of the two species. Nematocyst signatures of *Carcinactis ichikawai* Uchida, 1975: 598, *Verrillactis paguri, sensu* England, 1971: 32, and *C. dolosa* Riemann-Zürneck, 1975: 77, deduced from published data, are shown in Figures 40–42. The nematocyst differences indicate that the three species should be referred to three different genera and, therefore, that *C. dolosa* should be removed from *Carcinactis*. Riemann-Zürneck showed that *C. dolosa* has the same number of mesenteries at the margin as at the base (382 tentacles actually counted in 6 cycles of regularly arranged mesenteries ($6+6+12+24+48+96=192$ pairs, $=384$ tentacles), whereas both *Carcinactis* and *Verrillactis* have more mesenteries at the limbus than at the margin. *Carcinactis dolosa* has characters resembling those of species referred to *Actinothoe* Fischer, 1889, and *Sagartiogeton* Carlgren, 1924, though these genera are regarded as having only one type each of basitrich and of microbasic amastigophore in the acontia. These genera need to be examined further before a positive generic referal can be made. A provisional key to the genera of Sagartiidae to which these species might be referred is given in Figure 43.

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British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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